Estimation of Genetic-Gain Multipliers for Modeling Douglas-Fir Height and Diameter Growth

Peter Gould, Randy Johnson, David Marshall, and Greg Johnson

Abstract: Methods were developed to calculate genetic-gain multipliers for use in individual-tree models that predict periodic height and diameter growth of coast Douglas-fir *(Pseudotsuga menziesii* [Mirb.] Franco) in the Pacific Northwest. Genetic-gain multipliers are used in growth models that are typically based on extensive measurements of unimproved or "woods-run" stands, to adjust for the increased growth of stands generated from improved seedlots. First-generation progeny test data from multiple breeding zones in the Northwest Tree Improvement Cooperative were used. Data sets included initial heights and diameters and 5-year growth increments for 10- and 15-year-old trees that were identified by open-pollinated families. Nonlinear mixed-effect models were initially developed to predict the average growth of trees in all families, which, taken together, represented woods-run populations. Phenotypic differences in growth rates were then calculated at the family level. Differences among families in height and diameter growth rates were examined using methods from quantitative genetics and raw phenotypic values. Because gain in total height and diameter at age 10 years is currently the most widely available genetic information for improved Douglas-fir, equations were developed to predict genetic-gain multipliers from family breeding values for these traits. A verification procedure illustrated how incorporating multipliers in growth projections could reduce the mean-square error of predicted growth of selected families. FOR. SCI, 54(6):588-596.

Keywords: tree improvement, growth models, progeny tests, Pacific Northwest

THE WIDESPREAD USE of genetically improved seed sources in the Pacific Northwest and other regions may require revisions to yield tables and growth models that were based on information from wild or "woods-run" stands (Burkhart and Matney 1981). Projecting the growth of improved stands is important because genetic gain in traits such as height or diameter growth may lead to greater final harvest volumes and changes in management regimens, such as different thinning strategies and rotation lengths. In addition, growth projections are also needed for organizations to estimate their expected return on investments in tree breeding programs. The growth of woods-run stands of coast Douglas-fir *(Pseudotsuga menziesii* var menziesii [Mirb.] Franco) is fairly well understood and can be predicted by several regional growth models, some of which are in the public domain (e.g., ORGANON and FVS) (Donnelly 1997, Hann 2006). A major obstacle to accounting for genetic gain in growth models for the Pacific Northwest is a lack of research data on the growth of trees and stands generated from improved seedlots. Progeny tests currently provide measures of family performance based on the growth of individual trees in relative isolation or in a mix of superior and inferior families. However, progeny tests results are typically expressed in terms of percentage gain in total height or diameter at a given age. Individual-tree growth models that are used in the Pacific Northwest and elsewhere predict height and diameter growth increments, largely independent of tree age. Thus, the estimates of genetic gain that are typically produced by progeny tests cannot be readily incorporated into growth models.

Several approaches have been taken to incorporate the effects of genetic gain into growth models. A common approach is to estimate model parameters for individual families or groups of families. This approach has been applied to growth data for several species (Kurinobu and Shingai 1987, Danjon 1995), most notably loblolly pine *(Pinus taeda* L.) (Buford and Burkhart 1987, Knowe and Foster 1989, Sprinz et al. 1989, Adams et al. 2006). The height-age curve, often formulated as a site index curve, is a key component of many models. Genetic gain has been expressed by changing the height-age curve equation to reflect increased height-growth rates, asymptotic heights, or both (Buford and Burkhart 1987, Sprinz et al. 1989, Xie and Yanchuk 2003). Such changes will also affect diameter or basal area growth predictions that are based, in part, on height growth, total tree height, or site index. These growth equations may also need to be altered if genetic gain in diameter growth is not consistent with the gain implied by

Peter Gould, US Forest Service, PNW Research Station, Olympia Forest Sciences Laboratory, 3625 93rd Avenue SW, Olympia, WA 98512-Phone: (360) 753-7677; Fax: (360) 753-7737; pgould@fs.fed.us. Randy Johnson, US Forest Service-randyjohnson@fs.fed.us. David Marshall, Weyerhaeuser-David.Marshal12@weyerhaeuser.com. Greg Johnson, Weyerhaeuser- greg.johnson8@weyerhaeuser.com.

Acknowledgments: We thank Keith Jayawickrama and Terrance Ye of the Northwest Tree Improvement Cooperative for their assistance with this project. We also thank David Harm, Oregon State University, for his input during the initial stages of the project. This study is a product of the Sustainable Forestry component of Agenda 2020, a joint effort of US Forest Service Research and Development and the American Forest and Paper Association. Research partners include the Northwest Tree Improvement Cooperative at Oregon State University and the Pacific Northwest Research Station. Funds were provided by US Forest Service Research and Development. Data were obtained by various first-generation breeding cooperatives and independent breeding programs. Breeding values used in this study were predicted by the Northwest Tree Improvement Cooperative. Keith Jayawickrama, Doug Maguire, Terrance Ye, five anonymous reviewers, and an associate editor provided helpful comments on earlier drafts of this article. The article was prepared by federal employees and must remain in the public domain and cannot be copyrighted.

Manuscript received May 7, 2007, accepted July 18,2008

the change in height growth. Parameter estimation can potentially be used to incorporate detailed information on different families into growth models, but it requires extensive data sets. An ongoing modeling effort may also be required when new families are selected.

The use of genetic-gain multipliers is an approach that requires relatively little modification to existing growth models. Multipliers are calculated to reflect the relative difference in growth rate between improved and woods-run seed sources (Rehfeldt et al. 1991, Hamilton and Rehfeldt 1994, Carson et al. 1999). Predicted growth increments from existing models are then adjusted using multipliers to account for genetic gain in growth rate. As described by Carson et al. (1999), genetic-gain multipliers provide a means for extrapolating the results of progeny tests or deployment studies to existing growth models. They allow model users to take advantage of emerging, although incomplete, information on the characteristics of trees from improved seed sources. The individual-tree growth models that are commonly used in the Pacific Northwest and elsewhere predict growth increments based on initial tree size and other tree-level and stand-level factors. Genetic-gain multipliers for these models need to be able to accurately adjust predicted growth increments for trees that may already have different growth rates owing to differences in initial size and other factors.

The purpose of this study was to develop methods to estimate genetic-gain multipliers that are suitable for use in individual-tree growth models using data from progeny tests. Specifically, we developed methods to estimate genetic-gain multipliers for height and diameter growth using data from first-generation progeny tests of Douglas-fir. An extensive network of first-generation progeny tests of Douglas-fir, coordinated first by the InternationalForestry Association-US Forest Service Progressive Tree Improvement program, and later by the Northwest Tree Improvement Cooperative (NWTIC), has been established in the region. Superior parent trees have been identified and their breeding values *(BV)* for total height and diameter gain at age 10 years have been estimated. The expected gains in total height and diameter were used to predict genetic-gain multipliers for height and diameter growth because these gains have already been used to select parent trees and are currently the most detailed and widely used genetic information available. Our methods can also be used to estimate multipliers for height or diameter growth directly from progeny test results.

Methods

Data Sources

Data from a subset of the first-generation NWTIC breeding programs in Oregon and Washington were used for the analysis. Individual breeding programs were intended to cover a breeding zone, an area thought to contain a relatively homogeneous environment from which parent trees could be selected and their progeny could be planted while maintaining adaptability. Test sites were selected to represent the range of site conditions found within the breeding zone. Several sets of 30 to 50 open-pollinated families each were tested in each breeding zone. Most breeding programs used a reps-in-sets test design. At each test site, the set of families was planted using a noncontiguous plot design in three to four blocks (reps) that contained four to six trees from each family. This resulted in 12 to 20 trees established per family per site. The initial tree spacing of most site-set combinations ranged from 3.0 X 3.0 to 2.4 X 2.4 m, but three of those used for height-growth modeling had a spacing of 1.8 X 1.8 m. Very few tests included checklots or controls, but because parent trees were not selected on the basis of phenotype (i.e., no-intensive plus-tree selection), each set of families can be considered as a woods-run base population. Planting spots on "atypical" ground (e.g., burn piles, next to large stumps, or skid trails) were planted with ordinary nursery seedlings that were not included in the test data. These filler seedlings represent 20-25% of all planting spaces and were not measured.

Heights and diameters of all trees included in the modeling data sets were measured 10 and 15 years after sowing. Heights and diameters in some breeding zones were also measured 20 years after sowing. Family *BV* for height and diameter (percentage gain over the woods-run populations) were estimated by the NWTIC at age 10 years for all families using standard quantitative genetic methodologies (i.e., best linear unbiased predictions; White and Hodge 1989). Growth periods for the analyses were labeled by the first year of the growth period (e.g., the 10-year period included the initial heights and diameters at year 10 and the growth increments from year 10 to year 15). Data for each period were evaluated to ensure that at least 10 trees were measured for each family within a site-set combination, each family was measured in at least three site-set combinations, and at least 20 families were present within each site-set combination. Other measurements typically used in growth models, such as height to live crown and stand density (because of the presence of unmeasured filler trees) were not available. Site productivity was not estimated using site index because the trees were relatively young and their height growth was influenced by the unusually intensive site preparation treatments applied in the progeny tests. In addition, the different genotypes would potentially yield different estimates of site index.

Woods-Run Models

Woods-run models to predict height and diameter growth of individual trees were developed from the progeny test data. The predicted growth of all families was assumed to represent the mean growth of woods-run trees. Although existing growth models (e.g., ORGANON or FVS) would probably predict growth accurately on average, they were not used because the progeny test data did not include detailed tree-level (e.g., crown ratio) and stand-level information (e.g., basal area per hectare and site index). In addition, more precise estimates of the growth of woods-run trees were needed than could be produced by regional models. Precision was critical because family differences were expected to be small and could easily be obscured by model error.

After evaluation of several model forms, the combined

exponential-power function (Sit and Poulin-Costello 1994) was selected to model height and diameter increments for each period. This function allows predicted growth to increase, reach a peak, and then decrease with increasing initial height or diameter, which is a common pattern in tree growth. The models were

$$\beta_1 \cdot H_i^{\beta_2} \cdot \beta_3^{H_i} + \varepsilon_i, \quad (1)$$

$$\beta_1 \cdot D_i^{\beta_2} \cdot \beta_3^{D_i} + \varepsilon_i, \quad (2)$$

where ΔH_i is 5-year height increment for tree i, *Hi* is height of tree i at the beginning of the period, ΔD_i is 5-year diameter increment for tree i, D_i is diameter of tree i at the beginning of the period, $\beta_{1,2,3}$ are model coefficients, and ε_i is the residual for tree i,

Models were fit separately for the 10- and IS-year periods. The parameters β_1, β_2, and β_3 were fit as mixed parameters (i.e., containing both fixed and random effects). Random effects were estimated at the level of the site-set combination to ensure that differences among families within sets were not unduly obscured by variation among sets and among sites. Although the woods-run models did not explicitly account for important factors that influence growth, such as site productivity, social position, and stand density, the random effects help to capture the aggregate of effects that are attributable to differences among locations (Fang and Bailey 2001, Robinson and Wykoff 2004). These resulting models were complex, but parsimony was not an important consideration (unless it affected the convergence of parameter estimates) because the models were not meant to be general or used elsewhere, Model parameters were estimated using the nlme package (Pinheiro et al. 2006) in R (R Development Core Team 2006). The percentage of growth variance explained by the models was calculated using R^2_L, which is based on the difference in log-likelihood between full and intercept-only models (Magee 1990) and is an appropriate statistic for mixed-effects models (Kramer 2005).

Estimation of Genetic-Gain Multipliers

Using height growth as an example (the same analysis was also done for diameter growth), the phenotypic multiplier, *M,* is calculated for tree i by

$$M_i = \frac{\Delta H_i}{\Delta \hat{H}_i} \cdot 100\%, \quad (3)$$

where ΔH_i is observed height growth of tree i and $\Delta \hat{H}_i$ is predicted height growth of tree i under the woods-run model.

We define the genetic-gain multiplier, *Ma,* as the breeding value of *M. Ma* is calculated for a family from *M* and the heritability of *M* (Falconer and Mackay 1996):

$$Ma = 2' \bar{M} \cdot h^2_M, \quad (4)$$

where $\bar{M}$ is the mean of *M* among tested progeny and h^2_M is family-mean heritability of *M.* Similarly, the genetic gain due to selection of parents on phenotypic family means is predicted by

$$G_M = 2 \cdot i h^2_M \sigma_M, \quad (S)$$

where i is selection intensity and σ_M is the SD of family means of *M.*

Family breeding values are typically multiplied by 2 (Equation 4) to estimate parent breeding values under the assumption that the open-pollinated families are truly half-sib families. Similarly, the genetic gain of seedlots from an idealized clonal seed orchard (i.e., random mating and without pollen contamination) is two times the family gain (Equation 5). *M* and G_M would typically be converted to proportions for use in growth models so that without selection (i.e., woods-run seed sources) it would equal 1.0 and for improved seed sources would equal > 1.0.

Ma could be directly estimated from Equation 4 and G_M from Equation 5; however, this study is concerned with how selection on height *(H)* at age 10 years affects the rate of subsequent height growth. The expected gain in *M* when trees are selected for *H* is estimated using the equation for indirect selection (Falconer and Mackay 1996):

$$G_M = 2 \cdot i h_M h_H r_a \sigma_M, \quad (6)$$

where h_H is the square root of heritability for *H* at age 10 years, r_a is the genetic correlation between H and *M* calculated by $\sigma_{M_F H_F} / \sigma_{M_F} \sigma_{H_F}$, where $\sigma_{M_F H_F}$, σ_{M_F}, and σ_{H_F} are the family (family-within-set) component of covariance and square roots of the family variance components for *M* and *H.* The expected gain in *M* per unit gain in *H* is estimated by dividing both sides of Equation 6 by Equation 5 (substituting *H* for *M* in Equation 5). This yields a genetic slope coefficient to estimate G_M from G_H:

$$\alpha_G = G_M / G_H = r_a (h_M \sigma_M / h_H \sigma_H), \quad (7)$$

where σ_H is the SD of family means for height.

Estimates of α_G were calculated for each breeding zone and period using Equation 7 with G_M and G_H expressed as percent gains over their respective population means. PROC VARCOMP in SAS (SAS Institute, Inc., Cary, NC) was used to estimate genetic parameters (h^2_M, h^2_H, $\sigma_{M_F H_F}$, σ_{M_F}, and σ_{H_F}) from the variance components of the linear model,

$$Y_{hijkl} = \mu + S_i + T_j + R_{k(ij)} + (ST)_{ij} + F_{l(j)} + (FS)_{il(j)} + e_{hijkl}, \quad (8)$$

where Y_{ijkZ} is the observation on tree *h* in site i in set j in replicate *k* in family *t,* μ is the grand mean for the breeding zone, S_i is the effect of test site i, T_j is the effect of set j, $R_{k(ij)}$ is the effect of replicate *k* in site i and set j, $F_{Z(j)}$ is the effect of family *t* in set j, $(ST)_{ij}$ and $FS_{i/V)}$ are interaction terms, and e_{hijkZ} is residual error.

The dependent variable in Equation 8 was set to the individual-tree values of *M* to estimate h^2_M and σ_{M_F}. Tree height as the percent deviation from the replicate mean was used as the dependant variable to estimate h^2_H and σ_{H_F}. The sum of *M* and *H* were used to estimate $\sigma_{M_F H_F}$ using the relationship $\sigma_{MH} = ((J"(M+H)2 - \sigma^2_M - \sigma^2_H)/2$. Family-mean

heritabilities (Falconer and Mackay 1996) were calculated for each breeding zone by

$$h^2 = \frac{\sigma_F^2}{\sigma_F^2 + \sigma_{FS}^2/s + \sigma_e^2/sn}, \quad (9)$$

where σ_F^2 is variance due to family, σ_{FS}^2 is variance due to family x site interaction, σ_e^2 is within-family and site error variance, n is number of trees in each family at each test site, and s is number of test sites. The values of s and n in Equation 9 were approximated because the numbers of observations were not balanced among families and sites.

Estimation of Phenotypic Multipliers

The *BY* for total height (or diameter) at age 10 years is currently the most widely available genetic information on the parent trees tested by the NWTIC. The phenotypic multipliers (M) calculated from the progeny test data (described above) are currently the only estimates of how the growth of families deviates from expected growth under a woods-run model. A second approach to evaluating the relationship between height gain at age 10 years and *M* was taken using the ordinary least-squares (OLS) regression slope formula (Cook and Weisberg 1999)

$$\alpha_P = r_P(\sigma_M/\sigma_{BV}), \quad (10)$$

where r_p is the Pearson correlation coefficient of phenotypic values ($\omega_{M \cdot BV}/\sigma_M\sigma_{BV}$) and σ_{BV} is the SD of previously calculated *BY* for height at age 10 years.

Coefficients were estimated for the individual breeding zones, and all breeding zones were combined for each period. Coefficients for the combined breeding zones were also estimated using weighted least-squares (WLS) regression (Cook and Weisberg 1999) with weights = l/se(BV) to account for differences in the precision of the estimates of *BY* among breeding zones. The phenotypic coefficient (a_p) is similar to the genetic coefficient (aG)' but they are not identical. Because *BV* for height were calculated using the form of Equation 4, Equation 10 can be rewritten as

$$a_P = r_P \frac{\sigma_M}{h_H^2 \sigma_H}. \quad (11)$$

Because both traits are estimated from the same progeny tests, the correlation between traits is the correlation of phenotypic family means (r_p)' The correlation is given by (Burdon 1977)

$$r_p = r_a h_M h_H + r_e e_M e_H. \quad (12)$$

where r_a is the genetic correlation between traits, r_e is the correlation between environmental effects, $eM = (1 - h_M^2)^{1/2}$, $eH = (1 - h_H^2)^{1/2}$, and $eM' eH < 1.0$. Substitution Equation 12 into Equation 11 gives

$$a_P = (r_a h_M h_H + r_e e_M e_H) \frac{\sigma_M}{h_H^2 \sigma_H},$$

$$Qp \quad \left(r_a \frac{h_M \sigma_M}{h_H \sigma_H} \right) + r_e e_H e_M \frac{\sigma_M}{h_H \sigma_H},$$

$$a_p = a_G + r_e e_H e_M \frac{\sigma_M}{h_H \sigma_H}. \quad (13)$$

The estimates of Q_P provide a simple illustration of the relationship between predicted gain in height and *M,* but they are expected to be upwardly biased owing to the environmental correlation between *H and M.* If *M* and *BY* had been estimated from separate trials ($r_e = 0$) or if $h_M^2 = h_H^2 = 1$ ($eM = eH = 0$), then a_p and a_G would be equal.

Verification

A verification procedure was done to demonstrate the usefulness of *M* for improving growth estimates for selected families. First, the top 25% of families from each breeding zone were selected on the basis of their *BY* for height or diameter. Next, 1,000 samples, each consisting of 250 trees, were randomly selected from the subset of top families. The average growth increment was calculated for each random sample using the woods-run predictions and a range of values for *M. M* was calculated from

$$M = 1 + (a' BV)/lOO. \quad (14)$$

A range of values of α were tested. The span of α ranged from the case of a neutral multiplier (i.e., $\alpha = 0.00$ so that $M = 1.000$ for all *BV)* to the case where *M* was much larger than would generally be expected for a given BV. The average reduction in mean-squared error (MSE) due to *M* was calculated, and the percentage of the 1,000 cases for which *M* reduced the MSE below that of the woods-run model was also calculated.

Results

Data Summary and Woods-Run Models

Height-growth measurements from 2,485 families in 16 breeding zones were used for the 10-year period (Table 1).

Table 1. Summary of height-growth and diameter-growth datasets

Data set and period	Breeding zones	Families	Site-set combination	Obs	*H*	Δ*H*	*D*	Δ*D*
	.....(*n*).....				.....(m).....		.....(cm).....	
Height-growth								
10 yr	16	2,485	521	222,818	4.28	4.44	NA	NA
15 yr	1	90	15	7,571	9.60	4.49	NA	NA
Diameter-growth								
10 yr	7	1178	213	83,072	NA	NA	5.41	5.93
15 yr	2	321	48	20,396	NA	NA	12.14	4.27

Mean initial heights *(II)* and mean height-growth increments (Δ*H*) are shown for the height-growth data sets. Mean initial diameter *(D)* and mean diameter-growth increments (Δ*D*) are shown for the diameter-growth data sets. NA, not applicable.

Measurements from only 90 families in one breeding zone were available for the 15-year period. The mean initial tree height was 4.3 m for the lO-year period and 9.6 m for the 15-year period. The mean height growth increment for both periods was ~4.5 m. The lO-year diameter-growth data set was smaller and the 15-year data set was larger than the corresponding height-growth data sets. The mean diameter at 15 years was more than twice that at 10 years; however, the mean diameter increment was smaller for the 15-year period than for the lO-year period.

The woods-run height-growth models explained about 67% of the variation in height increment for the IO-year period and 18% for the 15-year period (Table 2). An analysis of residuals and the model parameters indicated that the 15-year model provided a good fit to the data, despite the low R_L^2. Growth was relatively invariant with initial height among sites and sets within sites for the IS-year data set, apparently because trees were reaching the height and age at which the height increment of Douglas-fir is at its maximum (Bruce 1981). As a result, the model would only converge with one random coefficient at most (β_1)' The ranges of random effects in the lO-year model were large relative to the fixed effects, indicating that differences between site-set combinations had a strong effect on height increments. The woods-run diameter-growth models explained about 60% of the variation in diameter increments for both periods. The ranges of random effects were also large relative to the fixed effects for the lO-year model. Smaller ranges of random effects were estimated for the 15-year model in which fewer breeding zones and site-set combinations were included.

Estimation of Multipliers

The genetic slope coefficients (α_G) for the 16 breeding zones analyzed for height growth during the lO-year period ranged from 0.14 to 0.59 (Table 3). The mean value of α_G for the lO-year period was 0.36. The phenotypic slope coefficients (α_P) were approximately equal to the genetic coefficients for all but one breeding zone and had a mean value of 0.35. The exception was breeding zone 3, for which α_P was considerably greater than α_G. The equations used to calculate α_G and α_P (Equations 7 and 11, respectively) have the same form and their components can be compared to identify how they affected the coefficient estimates. For example, r_G was greater than *rp* in all cases (see Equation 11), which increased the estimate of α_G relative to α_P. The SD of M (σ_M) appears in both equations, but it is multiplied by the square root of its heritability for α_G, which partially negates the differences between r_a and r_p. The SD of BV (σ_{BV}) that was used to estimate α_P was less than its counterpart in the genetic equation ($h_H\sigma_H$). The differences are attributable to two sources. First, the SDs of phenotypic height gains were multiplied by h_H^2 to yield BV. Because $h_H^2 < h_R$, σ_{BV} was reduced relative to $h_H\sigma_H$. Second, differences between the data set used in this study and the data set used previously to estimate BV (which included some families that were not suitable for modeling growth) may have also contributed to the differences, particularly in the case of the smaller value of σ_{BV} for breeding zone 3. Despite these differences, the two approaches yielded very similar estimates for the slope coefficients. Data from only one breeding zone were available for the 15-year period, and α_G and α_P were very similar.

Similar patterns were found in the estimates of α_G and α_P for the diameter-growth and height-growth data sets (Table 4). Values of α_G ranged from 0.10 to 0.51. The genetic and phenotypic approaches yielded similar results overall with average slope coefficient estimates of 0.31 and 0.36 for α_G and α_P, respectively, for the lO-year period and 0.48 and 0.45 for the 15-year period. As was found with the height-growth data sets, α_P was considerably greater than α_G for breeding zone 3, in large part because of the relatively low value of σ_{BV}.

The OLS and WLS estimates of phenotypic coefficients for the combined breeding zones for the 10- and 15-year periods were highly statistically significant ($P <$ 0.0001-0.009) (Table 5). All intercept estimates were within 1 SE of zero, indicating that the intercept could be dropped from the predictive equations without reducing the accuracy of M. The slope estimates were similar to the average values of α_G and α_P for the individual breeding zones, although the OLS and WLS slope estimates for lO-year height growth were somewhat lower. OLS and WLS slope estimates were compared between the 10- and 15-year periods using the general linear model (Neter et al. 1996). Only families that were measured in both periods were used for the comparisons. The differences between slope estimates were not statistically significant for either the height-growth (P = 0.42 and 0.45 for OLS and WLS, respectively) or diameter-growth models (P = 0.126 and 0.179 for OLS and WLS, respectively).

Verification

The verification procedure indicated that the MSE of the height-growth and diameter-growth increments predicted by

Table 2. Parameter estimates for the woods-run height-growth and diameter-growth models

	ß1		*ß2*		*ß3*		R_L^2
Period (yr)	Fixed	Random	Fixed	Random	Fixed	Random	(%)
Height-growth							
10	2.313 (0.034)	-1.781,2.141	0.955 (0.016)	-0.7731, 0.8375	0.862 (0.003)	-0.210, 0.148	67.3
15	0.601 (0.068)	-0.058, 0.065	1.371 (0.091)	NA	0.894 (0.009)	NA	17.6
Diabetes-growth							
10	3.305 (0.088)	-2.189, 3.274	0.354 (0.019)	-0.380, -0.681	1.006 (0.003)	-0.093, 0.076	60.6
15	0.111 (0.012)	-0.085, 0.215	1.849 (0.027)	-7.22 X 10-^{9},4.93 X 10^{-9}	0.941 (0.005)	-0.070, 0.048	59.0

Fixed effects are shown with 1 SE; random effects show minimum, maximum. The percentage of variation explained by the models (R_L^2) is shown.

Table 3. Results from the genetic and OLS approaches to calculate slope coefficients for predicting the percentage gain in height growth from lO-yr height gain

BZ	Period (yr)	Genetic				Phenotypic			
		h^2_M	h^2_H	r_G	α_G	σ_M	σ_{BV}	r_p	α_P
1	10	2.51	3.96	0.52	0.33	3.27	3.36	0.35	0.34
2	10	2.50	3.07	0.68	0.55	2.89	2.79	0.51	0.52
3	10	2.61	4.16	0.75	0.47	3.17	2.10	0.47	0.71
4	10	2.27	4.45	0.79	0.40	2.55	4.17	0.61	0.37
5	10	1.87	3.85	0.51	0.25	2.39	3.26	0.36	0.27
6	10	3.65	7.31	0.43	0.21	4.74	6.38	0.20	0.15
7	10	1.51	4.26	0.56	0.20	2.67	3.53	0.22	0.16
8	10	2.44	4.08	0.49	0.29	2.98	3.69	0.36	0.29
9	10	2.24	3.87	0.56	0.32	2.85	3.12	0.36	0.33
10	10	2.11	3.18	0.54	0.36	2.95	3.22	0.32	0.29
11	10	1.98	4.07	0.81	0.39	3.15	3.72	0.46	0.39
12	10	4.48	4.74	0.62	0.59	4.91	4.79	0.45	0.46
13	10	2.54	3.60	0.59	0.42	3.04	2.97	0.40	0.41
14	10	2.71	3.46	0.71	0.56	3.22	2.67	0.46	0.55
15	10	1.93	3.24	0.54	0.32	2.61	2.94	0.28	0.25
16	10	2.04	4.35	0.30	0.14	3.06	4.91	0.19	0.12
14	15	2.18	3.50	0.63	0.43	3.19	2.67	0.34	0.41

Results are given for each breeding zone (BZ) used in the analysis and growth period.

Table 4. Results from the genetic and OLS approaches to calculate slope coefficients for predicting the percentage gain in diameter growth from lO-yr diameter gain

BZ	Period (yr)	Genetic				Phenotypic			
		h^2_M	h^2_M	r_G	α_G	σ_M	σ_{BV}	r_p	α_P
2	10	3.68	4.22	0.59	0.51	4.08	3.81	0.42	0.45
3	10	2.66	4.51	0.51	0.30	3.09	1.89	0.29	0.48
6	10	4.12	9.13	0.33	0.15	4.80	6.55	0.31	0.23
9	10	2.53	4.25	0.17	0.10	3.23	3.18	0.22	0.23
10	10	2.77	3.57	0.39	0.31	3.42	3.49	0.33	0.32
11	10	3.78	4.74	0.55	0.44	4.56	4.40	0.47	0.48
15	10	3.32	4.54	0.46	0.33	4.03	3.96	0.30	0.30
2	15	6.05	3.82	0.25	0.40	6.30	3.81	0.11	0.18
3	15	4.23	4.21	0.55	0.55	5.06	1.90	0.27	0.72

Results are given for each breeding zone (BZ) and growth period used in the analysis.

Table 5. Coefficients (se) for the equation $M = \alpha_0 + \alpha_1 \cdot BV$ for the combined height-growth and diameter-growth datasets using ordinary-least squares (OLS) and weighted least-squares (WLS) with weights = 1/se(BV).

Period (yr)	α_0		α_1		r^2
	OLS	WLS	OLS	WLS	
Height-growth					
10	-0.04 (0.06)	-0.04 (0.055)	0.29 (0.02)	0.31 (0.02)	12.2
15	-0.08 (0.32)	-0.06 (0.29)	0.41 (0.12)	0.42 (0.12)	11.8
Diabetes-growth					
10	-0.07 (0.12)	-0.07 (0.11)	0.32 (0.03)	0.34 (0.03)	11.3
15	-0.08 (0.32)	-0.16 (0.32)	0.27 (0.10)	0.29 (0.11)	2.1

the woods-run models were reduced when M was used to adjust the initial predictions (Figure 1). A wide range of slope coefficients (α) was used to calculate M from the equation $M = 1 + (\alpha \cdot BV)/100$. The results from 1,000 random samples each consisting of 250 trees randomly selected from the top 25% of families from each breeding zone (as measured by their BV for total height or diameter) demonstrated the sensitivity of growth predictions to the exact value of α used to calculate M. The greatest reduction in MSE occurred when α was equal to the phenotypic slope estimates, but the reduction in MSE was only moderately sensitive to α. Thus, similar reductions in MSE occurred for height and diameter growth during the10-year period when α ranged from ~0.26 to 0.36. Because height and diameter growth for the top families was generally underpredicted by the woods-run model, a small value of α reduced MSE in nearly 100% of the 1,000 test cases. Applying M calculated within the range of α estimated by the genetic and phenotypic approaches (i.e., 0.29-0.36) reduced MSE in more than 70% of cases. Growth was overpredicted in an increasingly large percentage of cases

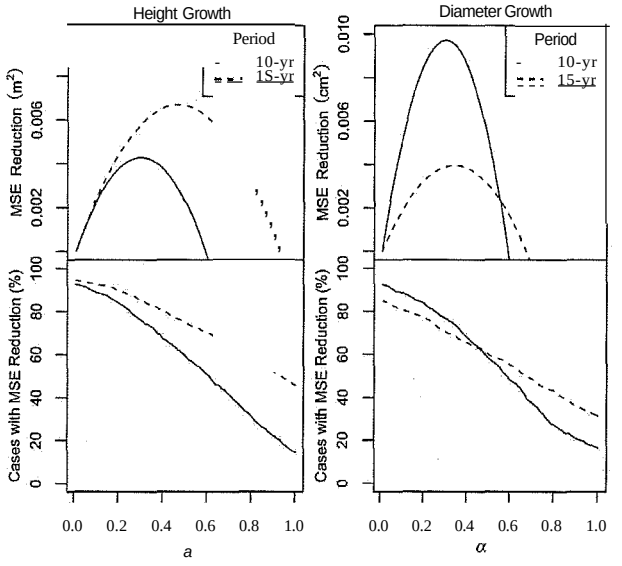

Figure 1. Verification of the effectiveness of growth multipliers *(M)* for reducing the MSE of predicted height growth (left) and diameter growth (right) during the 10· and 15-year periods. Results are based on 1,000 random samples each of 250 trees from the top families in each breeding zone. The average total reduction in MSE when M was calculated by $M = \alpha . BV$ (where BV is the breeding value for total height or diameter at age 10 years) is shown at top and the percentage of cases where M reduced MSE is shown below.

as α increased; thus the percentage of cases in which MSE was reduced decreased considerably with excessively large values of α.

Discussion

The slope coefficients listed in Tables 3, 4, and 5 were derived using different approaches, but they yielded similar results. The genetic approach yielded an average value of 0.36 for height growth during the lO-year period, while the phenotypic approach for the combined data sets yielded values of 0.29 using OLS and 0.31 using WLS. For diameter growth during the lO-year period, the genetic approach yielded an average value of 0.31, whereas the OLS and WLS methods yielded values of 0.32 and 0.34, respectively, for the combined data sets. The genetic coefficients for the 15-year period were greater than those for the lO-year period, but there was not a statistically significant difference between the phenotypic estimates for the two periods based on the analysis of families common to both periods. We recommend that modelers use the lO-year average genetic coefficients for calculating M from expected gain in height or diameter at age 10 year. Whereas the phenotypic coefficients provide the best fit to the data from the progeny tests, the genetic values provide the best predictions of genetic gain in growth rates in future stands (Falconer and Mackay 1996). These values were calculated from larger data sets than those used to calculate the 15-year values and should provide the best predictions of the gain in M due to selection for total height or diameter. Results of the verification procedure suggest that MSE can be reduced for both time periods using a single value of M. We recommend that modelers assume that M remains constant for stands beyond age 10 years until more information becomes available. These results are consistent with those of a similar study focused on the growth of improved radiata pine *(Pinus radiata* D. Don) which showed that genetic-gain multipliers did not decline over a similar period (Carson et al. 1999). Because predicting volume at the end of the rotation is the goal of many growth projections, model users will routinely extrapolate these results beyond the period examined in this study. Caution is warranted, particularly for longer rotations. Additional data should be analyzed as it becomes available to determine whether this assumption holds true. Early genetic gain in height or diameter (up to age 10 years) should also be included in growth projections. A workable approach may be to integrate early genetic gain into stand establishment models or submodels on the basis of the expected gain at 10 years. This model output would then be used to project future growth using an individual-tree model with multipliers.

Several approaches could be used to calculate M for inclusion in growth projections. M could be predicted directly from progeny tests results as a breeding value for individual parent trees or families using a methodology similar to that outlined in this study (Equations 3, 4, and 5). In the present study, it was assumed that families had already been selected or would be selected on the basis of total height or diameter at 10 years and breeding values for these traits would be the most readily available measure of genetic value. In this case, M could be predicted on the basis of the existing breeding values. Ultimately, multipliers will be applied to genetically improved stands, and M will need to be calculated as a measure of the genetic worth of the seedlot used to generate a particular stand (Xie and Yanchuk 2003). M can be calculated from the predicted gain in lO-year height or diameter for the seedlot or from breeding values of M for the parent trees. In either case, pollen contamination and other factors should be considered when gain in total height and diameter and values of M for height and diameter growth are estimated. The values of M will vary according to the predicted gain in height or diameter of a particular seedlot. For comparison with other studies, Carson et al. (1999) calculated a height-growth multiplier of 1.051 for improved radiata pine from open-pollinated seed orchards. Hamilton and Rehfeldt (1994) calculated multipliers of 1.072 for height and 1.092 for diameter for open-pollinated ponderosa pine *(Pinus ponderosa* Dougl. ex Laws.) families. Using the mean genetic coefficients for the lO-year period in Equation 14, height-growth multipliers of 1.051 and 1.072 would be appropriate for Douglas-fir seedlots with lO-year height gains of 14 and 20%. A diameter gain of 30% would yield a diameter-growth multiplier of 1.092. The effects of the multipliers need to be evaluated after accounting for any prior gain that is expected to occur before the beginning of the projection period. Growth models can then be used to estimate the ultimate volume gain at the end of the rotation; however, such volume projections should be interpreted with caution because they will typically run beyond the period examined in this study.

The methodological approach used in this study was largely dictated by the available data. One question raised

by the approach is how the genetic-gain multipliers will perform in regional growth models such as ORGANON or FVS (Donnelly 1997, Hann 2006). In a similar study (Carson et al. 1999), an existing regional growth model was used to predict woods-run growth, and predicted growth was then compared with the actual growth of improved seedlots to yield genetic-gain multipliers. This approach was not possible in the present study because stand- and tree-level variables used in regional growth models were not measured in the progeny tests. However, the multipliers represent the simple ratio between woods-run growth and the growth of a particular seedlot. Consequently, they should be appropriate for use in any individual-tree model that produces unbiased growth estimates for woods-run populations. When incorporated into growth models, genetic-gain multipliers are expected to accelerate the development of improved seedlots but not to change the overall patterns of tree and stand development. Althoughthis effect is apparent, problems may be identified in specific growth models, and caution is warranted. For example, volume estimates for improved stands may need to be reevaluated if existing equations are unable to accurately account for changes in the height/diameter ratio because of different levels of genetic gain for these traits.

The experimental design of the present study (noncontiguous individual-tree plots) was not optimal for modeling genetic gain and may also have some effect on the accuracy of the estimates of *M.* Stand age and density can affect the expression of genotypic differences, particularly in diameter-growth rates (Nance and Wells 1981, Magnussen 1989). Block-plot trials, in which families with similar genetic gain are planted together, better replicate the operational deployment of improved seedlots. In the NWTIC data sets, 10-year genetic gain could have been inflated relative to realizable gain if size differences between families resulted in a competitive advantage among trees in the top families and a concurrent disadvantage among those in families that performed poorly. However, the actual competitive advantage of trees in the top families was probably small in this case. Open-pollinated families of Douglas-fir contain, on average, about 95% percent of the phenotypic variation found within the larger population through age 20 years (Johnson et al. 1997). There is a great deal of overlap in height and diameter distributions (and presumably competitive abilities) among families despite differences in family means. In addition, the progeny tests in this study had wide initial spacings relative to those of other studies (e.g., Magnussen 1989), suggesting that competition was not as dominant a factor in determining tree size and growth rates as has been reported at closer spacings. Early results from Douglas-fir block-plot trials also indicate that individual-tree plots can produce unbiased estimates of realized gain (St. Clair et al. 2004) More important to this study was the potential effect of competition on the estimation of *M* at the family level. *M* was estimated after accounting for initial size and differences in density and other factors between plantings (via random effects). Thus, the impact of competition on the estimates of *M* was probably minimal. Block-plot trials are still urgently needed to test and refine our results, particularly for later stages of stand development during which competition is more important. In addition, block-plot trials are needed to better understand other differences between genotypes, such as differences in maximum density, asymptotic height, and stand volume. One such block-plot trial was established in 1997 (St. Clair et al. 2004) and another in 2005 and 2006 (Jayawickrama 2006).

The precision of the estimates of *BV* and *M* are also important to growth modeling. Parent trees can be selected and breeding values can be estimated with an acceptable level of error using relatively small numbers of progeny in well-designed progeny tests. However, error in the estimates of *BV* and *M* take on greater importance when they are used in growth models. The OLS and WLS estimates of α were affected by error in *BV* because both regression approaches assume that the independent variable was measured without error. Error in the independent variable reduces the magnitude of the regression slope coefficient (Schaalje and Butts 1993, Buonaccorsi 1995). In most growth models, the prediction error in *M,* as well as measurement error in other variables, will not be recognized. However, it will be manifested by greater error in growth predictions. For the purpose of projecting the growth of improved seedlots, it is clearly important to estimate *BV* and *M* as precisely as possible.

Conclusions

The results presented here provide a new method for calculating multipliers for height and diameter growth of improved Douglas-fir in the Pacific Northwest. They can be applied to parents with known breeding values for total height and diameter at age 10 years or to seedlots with predicted levels of gain for these traits. Growth differences between woods-run and improved seedlots appear to remain fairly constant from ages 10-20 years. On the basis of this information, we recommend calculating multipliers using the average genetic regression coefficients for the lO-year period to project the growth of stands that are 10 years or older. Users should be aware that growth projections will routinely exceed the period spanned by the data used to predict the multipliers and caution should be exercised. Tree lists created from stand inventories provide the best information for projecting stands 10 years or older. Representative tree lists or those created by stand establishment models to reflect woods-run populations can potentially be adjusted on the basis of the expected gain of a seedlot in total height and diameter at 10 years. Including this early gain will probably be important to accurately predict long-term stand development.

Literature Cited

ADAMS, J.P., T.G. MATNEY, S.B. LAND, JR., K.L. BELLI, AND H.W. DUZAN, JR. 2006. Incorporating genetic parameters into a loblolly pine growth-and-yield model. *Can. J. For. Res.* 36:1959-1967.

BRUCE, D. 1981. Consistent height-growth and growth-rate estimates for remeasured plots. *For. Sci. 27:711-725.*

BUFORD, M.A., AND H.E. BURKHART. 1987. Genetic improvement effects on growth and yield of loblolly pine plantations. *For. Sci. 33:707-724.*

BUONACCORSI, J.P. 1995. Prediction in the presence of measurement error: General discussion and an example predicting defoliation. *Biometrics 51:1562-1569.*

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

BURKHART, H.E., AND T.G. MATNEY. 1981. Growth and yield modeling-A place for genetic improvement effects. P. 6-17 in *Proc. of the 16th Southern tree improvement conference.* Blacksburg, VA.

CARSON, S.D., O. GARCIA, AND J.D. HAYES. 1999. Realized gain and prediction of yield with genetically improved *Pinus radiata* in New Zealand. *For. Sci. 45:186-200.*

COOK, RD., AND S. WEISBERG. 1999. *Applied regression including computing and graphics.* Wiley, New York, NY.

DANJON, F. 1995. Observed selection effects on height growth, diameter and stem form in maritime pine. *Silv. Genet.* 44:10-19.

DONNELLY, D.M. 1997. *PacifiC Northwest Coast Variant of the Forest Vegetation Simulator.* US For. Servo WO Forest Management Service Center. 51 p.

FALCONER, D.S., AND T.F.C. MACKAY. 1996. *Introduction to quantitative genetics.* Longman Group Limited., Harlow, UK.

FANG, Z., AND R.L. BAILEY. 2001. Nonlinear mixed effects modeling for slash pine dominant height growth following intensive si1vicultural treatments. *For. Sci. 47:287-300.*

HAMILTON, DA, JR., AND G.E. REHFELDT. 1994. Using individual tree growth projection models to estimate stand-level gains attributable to genetically improved stock. *For. Eco/. Manag.* 68:189-207.

HANN, D.W. 2006. *Organon user's manual edition* 8.2. Oregon State University College of Forestry. 129 p.

JAYAWICKRAMA, K.J. 2006. *Northwest Tree Improvement Cooperative annual report, April* 1, *2005-June 30, 2006.* Available online at www.fsl.orsLedu/nwtic/Annual_Reports/nwtic_2005.pdf; last accessed Apr. 13, 2007.

JOHNSON, G.R., R.A. SNIEZKO, AND N.L. MANDEL. 1997. Age trends in Douglas-fir genetic parameters and implications for optimum selection age. *Silv. Genet. 46:349-358.*

KNOWE, SA, AND G.S. FOSTER. 1989. Application of growth models for simulating genetic gain of loblolly pine. *For. Sci.* 35:211-228.

KRAMER, M. 2005. R-squared statistics for mixed models. P. 148-160 in *Proc. of the 17th Annual Kansas State University conference on applied statistics in agriculture,* Boyer, J.E., Jr. (ed.). Kansas State University, Manhattan, KS.

KURINOBU, S., AND Y. SHINGAI. 1987. Stand-volume prediction of improved trees based on the realized gain in progeny tests of hinoki *(Chamaecyparis obtusa* Endl.). *Silv. Genet. 36:* 159-164.

MAGEE, L. 1990. R^2 measures based on Wald and likelihood ratio joint significance tests. *Am. Statistician 44:250-253.*

MAGNUSSEN, S. 1989. Effects and adjustments of competition bias in progeny trials with single-tree plots. *For.* Sci. 35:532-547.

NANCE, W.L., AND 0.0. WELLS. 1981. Estimating volume potential in genetic tests using growth and yield models. P. 39-46 in *Proc. of the 16th Southern tree improvement conference.* Blacksburg, VA.

NETER, J., M.H. KUTNER, C.J. NACHSHEIM, AND W. WASSERMAN. *1996. Applied linear statistical models,* 4th ed. WCB McGraw Hill, New York, NY.

PINHEIRO, J., D. BATES, S. DEBRoy, AND D. SARKAR. 2006. *nlme: Linear and nonlinear mixed effects models,* R package version 3.1-73.

R DEVELOPMENT CORE TEAM. 2006. *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. Available online at www.R-projecLorg; last accessed Jan. 28, 2008.

REHFELDT, G.E., W.R WYKOFF, R.J. HOFF, AND R.J. STEINHOFF. 1991. Genetic gains in growth and simulated yield of *Pinus monticola. For. Sci. 37:326-342.*

ROBINSON, A.P., AND W.R WYKOFF. 2004. Imputing missing height measures using a mixed-effects modeling strategy. *Can. J. For. Res. 34:2492-2500.*

SCHAALJE, G.B., AND RA BUTTS. 1993. Some effects of ignoring correlated measurement errors in straight line regression and prediction. *Biometrics.* 49:1262-1267.

SIT, V., AND M. POULIN-COSTELLO. 1994. *Catalog of curves for curve fitting.* Province of British Columbia Ministry of Forestry, Victoria, BC, Canada.

SPRINZ, P.T., C.B. TALBERT, AND M.R. STRUB. 1989. Height-age trends from an Arkansas seed source study. *For. Sci.* 35:677-691.

ST. CLAIR, J.B., N.L. MANDEL, AND K.J.S. JAYAWICKRAMA. 2004. Early realized genetic gains for coastal Douglas-fir in the Northern Oregon Cascades. *West. J. App/. For. 19:195-201.*

WHITE, T. L., AND G. R. HODGE. 1989. Predicting breeding values with applications in" forest tree improvement. Kluwer Academic Publishers, Dordrecht, Netherlands.

XIE, c.Y., AND A.D. YANCHUK. 2003. Breeding values of parental trees, genetic worth of seed orchard seedloIs, and yields of improved stocks in British Columbia. *West. J. App/. For.* 18:88-100.