

Annualized diameter and height growth equations for Pacific Northwest plantation-grown Douglas-fir, western hemlock, and red alder

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Abstract

Simulating the influence of intensive management and annual weather fluctuations on tree growth requires a shorter time step than currently employed by most regional growth models. High-quality data sets are available for several plantation species in the Pacific Northwest region of the United States, but the growth periods ranged from 2 to 12 years in length. Measurement periods of varying length complicate efforts to fit growth models because observed growth rates must be interpolated to a common length growth period or those growth periods longer or shorter than the desired model time step must be discarded. A variation of the iterative technique suggested by Cao [Cao, Q.V., 2000. Prediction of annual diameter growth and survival for individual trees from periodic measurements. *Forest Sci.* 46, 127–131] was applied to estimate annualized diameter and height growth equations for pure plantations of Douglas-fir, western hemlock, and red alder. Using this technique, fits were significantly improved for all three species by embedding a multi-level nonlinear mixed-effects framework (likelihood ratio test: $p < 0.0001$). The final models were consistent with expected biological behavior of diameter and height growth over tree, stand, and site variables. The random effects showed some correlation with key physiographic variables such as slope and aspect for Douglas-fir and red alder, but these relationships were not observed for western hemlock. Further, the random effects were more correlated with physiographic variables than actual climate or soils information. Long-term simulations (12–16 years) on an independent dataset using these annualized equations showed that the multi-level mixed effects models were more accurate and precise than those fitted without random effects as mean square error (MSE) was reduced by 13 and 21% for diameter and height growth prediction, respectively. The level of prediction error was also smaller than an existing similar growth model with a longer time step (ORGANON v8) as the annualized equations reduced MSE by 17 and 38% for diameter and height growth prediction, respectively. These models will prove to be quite useful for understanding the interaction of weather and silviculture in the Pacific Northwest and refining the precision of future growth model projections.

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1. Introduction

Over the last few decades rotation lengths in plantations of the Pacific Northwest (PNW) have significantly decreased and are currently ranging from 30 to 50 years (Adams et al., 2005). Growth and yield models in the region, however, continue to use a 5–10 year time step. With the shorter rotations, treatment windows for silvicultural activities such as fertilization,

thinning, and pruning are also shortening, and are often less than 5 years, especially on more productive sites. The longer model time steps also make it difficult to forecast silvicultural treatment effects accurately or investigate the role of annual climate fluctuations on growth (e.g. Henning and Burk, 2004). For example, Johnson (2005) recently found a very wide range (1.3–2.3-fold difference) of predicted responses to thinning, fertilization, and the combination of these treatment for six commonly used PNW empirical growth models. These large differences among models can partially be attributed to their inability to capture the short-term stand dynamics following intensive treatment. As management practices continue to

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intensify and rotations remain relatively short in this region, the need for annual diameter and height growth equations is apparent.

The primary difficulty in developing annual equations is that most permanent plots are remeasured on a 2–6 year cycle. Shorter measurement cycles are usually not favored because the effect of measurement error can greatly bias results (e.g. Snowdon, 1987). McDill and Amateis (1993) evaluated several different methods to fit annual growth models from periodic measurements and found two interpolation methods to work better than simple averaging. Cao (2000) generalized these conclusions and recently presented a method to simultaneously develop annual individual tree diameter and height growth and survival equations from periodic measurements (Cao et al., 2002). This method has been successfully used for European beech [*Fagus sylvatica* L.] (Nord-Larsen, 2006), loblolly pine [*Pinus taeda* L.] (Cao, 2000, 2004; Cao et al., 2002), longleaf pine [*Pinus palustris* Mill.] (Cao et al., 2002), Norway spruce [*Picea abies* (L.) H. Karst] (Johannsen, 1999), and oak [*Quercus robur* L. and *Quercus petraea* L.] (Johannsen, 1999).

However, these previous analyses have not accounted for the sampling structure of these types of data. In addition to having multiple measurements made on trees over varying time periods, these trees are often nested within plots and perhaps more grouping levels. The repeated measures and hierarchical nature of these data result in autocorrelation violating the assumptions of least squares. One approach to remedying this is to directly model the covariance structure via a continuous autoregressive process (Gregoire, 1987). This approach adequately accounts for spatial and temporal correlation among measurements but may not represent the hierarchical nature of the data. A second approach is to introduce one or more random effects on a subset of parameters at each level of nesting. Each approach has been effective in reducing the impact of autocorrelation on hypothesis testing (Hall and Bailey, 2001; Hibbs et al., 2007). However, the latter approach may better account for the complex covariance structure and provide better predictions (Hall and Bailey, 2001). Moreover, the random effects approach has the additional appeal of permitting the evaluation of plot and site covariates not typically included within the models.

The primary objective of this study was to extend Cao's (2000) approach to hierarchical data in developing annualized diameter and height growth equations from periodic measurements in pure, untreated plantations of coastal Douglas-fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco], western hemlock [*Tsuga heterophylla* (Raf.) Sarg], and red alder [*Alnus rubra* Bong.]. Specific objectives were to: (i) determine whether the combination of Cao's (2000) technique and hierarchical approaches produce biologically consistent parameters estimates; (ii) compare fits and predictions with generalized nonlinear least squares (GNLS) and multi-level nonlinear mixed effects (NLME); (iii) test the physiographic variables on diameter and height growth of these three species by regressing the installation

random effects on these variables; and (iv) evaluate these annualized equations against a commonly used regional growth model.

2. Methodology

2.1. Data sets

Data for this study came from existing permanent plots established by three PNW research cooperatives. The Douglas-fir growth data were from the Stand Management Cooperative (SMC; University of Washington) and the Swiss Needle Cast Cooperative (SNCC; Oregon State University). The western hemlock data were obtained solely from the SMC database. The red alder growth data came from the SMC and the Hardwood Silviculture Cooperative (HSC; Oregon State University). In all cases, only pure, untreated plots with at least 10% of the sampled trees having breast-height age, height (HT), and height to crown base (HCB) measurements were used. A brief description of each database is given below.

2.1.1. Stand Management Cooperative (SMC)

Since its establishment in 1985, the SMC (<http://www.cfr.washington.edu/research.smc/>) has maintained a database representing 435 installations in British Columbia, Washington, and Oregon (Maguire et al., 1991). The primary sampling population was from plantation-grown Douglas-fir in western Oregon, Washington, and British Columbia, but some work was also done in western hemlock and red alder plantations. For this analysis, Douglas-fir and western hemlock data were extracted from the Type I and III installations. Type I installations were established as square 0.2-ha plots in existing plantations and have received designed sets of silvicultural treatments since plot establishment in the late 1980s and early 1990s. Type III installations were established as initial spacing trials with six densities ranging from 247 to 3048 trees per ha. Plot size varied from 0.086 ha at the highest density to 0.202 ha at the lowest density. In addition, plots from four western hemlock installations were included in the analysis. These plots were established in 1980 during Phase IV of the Regional Forest Nutrition Research Project (RFNRP; University of Washington) and were designed to test growth responses to fertilization in precommercially thinned plantations. The red alder data were collected from two installations established in 1980 as part of a Department of Energy project to examine the implications of whole tree harvesting on nutrient capital.

2.1.2. Swiss Needle Cast Cooperative (SNCC)

The SNCC established 76 permanent plots (0.08 ha) in 1998 to represent relatively young, e.g. 10–30-year-old, Douglas-fir plantations, with varying levels of SNC (Maguire et al., 2002) (<http://www.cof.orst.edu/coops/sncc/>). In addition, 22 untreated plots (0.08 ha) from a precommercial thinning study and 30 untreated plots (0.2-ha) from a commercial thinning study were also included. The former

permanent plots were established in 10–15-year-old plantations in 1998, and the latter were established in 30–60-year-old plantations in 2002 (Mainwaring et al., 2005), respectively. Each plot has been assessed annually for SNC severity and measured for growth every 2 years. Preliminary analysis found very little bias across a range of SNC severities with a fitted regional growth equation and, hence, all untreated plots were included in the final analysis.

2.1.3. Hardwood Silviculture Cooperative (HSC)

The HSC was first established in 1988 and maintains the oldest and most extensive red alder database available (<http://www.cof.orst.edu/coops/hsc/>). The growth data were collected from 26 Type 2 installations located between Coos Bay, Oregon and Sayward on Vancouver Island, British Columbia. Plots (0.13 ha in size) were established between 1989 and 1997, and each installation included at least five different initial densities ranging from 254 to 3048 trees per ha across a range of site fertility classes.

2.2. Growth modeling

A subsample of trees were measured for HT and HCB on each plot, so tree attributes were estimated for the remaining trees by fitting equations for each species. Preliminary analysis indicated that a mixed models framework similar to the one described by Robinson and Wykoff (2004) significantly improved imputation. The final models were:

$$HT = 1.37 + \exp(\beta_{10} + b_{1i} + b_{1j} + \beta_{11}DBH^{\beta_{12}}) + \varepsilon_1 \quad (1)$$

$$HCB = \frac{HT}{1 + \exp(\beta_{20} + b_{2i} + b_{2j} + \beta_{21}HT + \beta_{22}CCFL + \beta_{23}\log(SBA) + \beta_{24}(DBH/HT) + \beta_{25}(SI - 1.37))} + \varepsilon_2 \quad (2)$$

where DBH is diameter at breast height (1.37 m), CCFL is crown competition factor in trees of larger diameter than the subject tree (Krajicek et al., 1961; Hann et al., 2003), SBA is stand basal area per hectare, SI is species-specific site index (described below), β_{ij} 's are model fixed parameters, b_{1i} , b_{1j} , b_{2i} , and b_{2j} , are random intercept terms for the i th installation and j th plot, and ε_1 and ε_2 are within plot random error terms that are assumed to be $N(0, \sigma_i^2)$. All random effects were tested for significance with likelihood ratio tests using a significance level of 0.05 (Pinheiro and Bates, 2000). The best linear unbiased predictors (BLUP) were estimated for each plot and used to fill in the missing tree attributes. Crown ratio (CR) was then calculated as $1 - HCB/HT$.

Varying definitions of crown base were used in each of the databases, even for a given species. For example, Douglas-fir HCB in the SMC database was defined as the lowest contiguous whorl of at least two live branches (compacted crown ratio), while HCB in the SNCC database was defined as the lowest live branch (uncompacted crown ratio). After predicting missing CR's from (2), all plots where compacted crown ratio was

measured and predicted were converted to uncompacted crown ratio using the equations of Monleon et al. (2004).

In addition to SBA and CR, several other growth predictor variables were derived including SI, basal area in trees with a DBH larger than the subject tree (BAL), and the percent crown closure of the plot at the tip of the subject tree (CCH) (Hann et al., 2003). Values of SI were determined using equations that require breast height age and top height for the 100 largest-diameter trees per ha of the target species. SI at 50 years base age for Douglas-fir was calculated by solving Bruce's (1981) dominant height equation. The Bonner et al. (1995) equation was used for western hemlock. Three red alder site index equations were considered because no previous individual tree growth equation existed. The equation of Nigh and Courtin (1998) was used in the final equations because it had a base age 25 years and preliminary analysis suggested it had a higher correlation with growth than equations presented in Harrington (1986) and Harrington and Curtis (1986).

SBA was determined by summing the product of the cross-sectional area at breast height and expansion factor for each tree on the plot of interest basal area in larger trees (BAL) was calculated for each tree by summing the product of cross-sectional area at breast height and expansion factor of all trees on the plot of interest having larger DBH values than the subject tree. For each tree, CCH was calculated by estimating crown widths for all other trees on the plot at the height of the subject tree. Crown profile equations presented in Hann (1999), Marshall et al. (2003), and Hann (1997) for Douglas-fir, western hemlock, and red alder, respectively, were used to calculate crown width, which was converted to crown area by using the formula for the area of a circle. The crown areas were multiplied by the tree expansion factor, summed across all subject trees on the plot with a height greater than the height of the sample tree, and then expressed as a percentage of ground area covered to obtain CCH values for each tree. This procedure was repeated for all trees on a plot.

2.2.1. Diameter growth

After evaluating several parameterizations, diameter growth was modeled using the method of Cao (2000) and the form suggested by Hann et al. (2003):

$$\begin{aligned} \Delta DBH = & \exp\left(\beta_{30} + \beta_{31}\log(DBH + 1) + \beta_{32}DBH^2\right. \\ & + \beta_{33}\log\left(\frac{UCR + 0.2}{1.2}\right) + \beta_{34}\log(SI - 1.37) \\ & \left. + \beta_{35}\frac{BAL^2}{\log(DBH + 5)} + \beta_{36}\sqrt{SBA} + \beta_{37}I_{CR}\right) + \varepsilon_{3a} \end{aligned} \quad (3a)$$

where ΔDBH is the annual diameter growth in cm, UCR is uncompacted crown ratio, I_{CR} is an indicator variable having a value of 1 if CR was not measured and 0 otherwise, the β_{ij} 's are parameters to be estimated from the data using GNLS, and

$\varepsilon_{3a} \sim N(0, \sigma_{3a}^2)$. The model was also fit using NLME:

$$\begin{aligned} \Delta\text{DBH} = \exp & \left(\beta_{30} + b_{3i} + b_{3j} + \beta_{31} \log(\text{DBH} + 1) \right. \\ & + \beta_{32} \text{DBH}^2 + \beta_{33} \log \left(\frac{\text{UCR} + 0.2}{1.2} \right) \\ & + \beta_{34} \log(\text{SI} - 1.37) + \beta_{35} \frac{\text{BAL}^2}{\log(\text{DBH} + 5)} \\ & \left. + \beta_{36} \sqrt{\text{SBA}} + \beta_{37} I_{\text{CR}} \right) + \varepsilon_{3b} \end{aligned} \quad (3b)$$

where the β_{ij} 's are annualized parameters to be estimated using NLME, b_{3i} , and b_{3j} are random intercept terms for the i th installation and j th plot, and ε_{3b} is the within tree error. For western hemlock, only an installation random effect was estimated as only one plot was established at each installation.

2.2.2. Height growth

Height growth was modeled as the product of potential height growth, the theoretical estimate of height growth of a dominant tree of that size (Wensel et al., 1987), and a height growth modifier:

$$\Delta\text{HT} = \text{PHG} \times \text{HMOD} \quad (4)$$

where ΔHT is the annual height growth, PHG is potential height growth, and HMOD is the height growth modifier. PHG was calculated as follows:

$$\text{PHG} = f_{\text{SPP}}(\text{SI}_{\text{SPP}}, \text{GEA} + 1.0) - \text{HT} \quad (5)$$

where f_{SPP} is the dominant height growth equation for species and GEA is the calculated growth effective age (Hann and Ritchie, 1988). Dominant height growth equations for the three species were Bruce's (1981), Bonner et al.'s (1995), and Nigh and Courtin (1998) for Douglas-fir, western hemlock, and red alder, respectively. GEA is defined as the age of a dominant tree with the same height and site as the tree of interest:

$$\text{GEA} = f_{\text{SPP}}^{-1}(\text{SI}_{\text{SPP}}, \text{HT}). \quad (6)$$

The following modifier equation form was used for each species (Hann and Ritchie, 1988; Hann et al., 2003):

$$\begin{aligned} \text{HMOD} = \beta_{70} [\beta_{71} e^{\beta_{72} \text{CCH}} \\ + (e^{\beta_{73} \sqrt{\text{CCH}}} - \beta_{71} e^{\beta_{72} \text{CCH}}) e^{-\beta_{74} (1 - \text{UCR})^2 e^{\beta_{75} \sqrt{\text{CCH}}}}] + \varepsilon_{7a} \end{aligned} \quad (7a)$$

where the β_{ij} 's are parameters to be estimated from the data using GNLS, and $\varepsilon_{7a} \sim N(0, \sigma_{7a}^2)$. The model was also fitted using NLME:

$$\begin{aligned} \text{HMOD} = (\beta_{70} + b_{7i} + b_{7j}) [\beta_{71} e^{\beta_{72} \text{CCH}} \\ + (e^{\beta_{73} \sqrt{\text{CCH}}} - \beta_{71} e^{\beta_{72} \text{CCH}}) e^{-\beta_{74} (1 - \text{UCR})^2 e^{\beta_{75} \sqrt{\text{CCH}}}}] + \varepsilon_{7b} \end{aligned} \quad (7b)$$

where the β_{ij} 's are annualized parameters to be estimated with NLME, b_{7i} , and b_{7j} are random intercept terms for the i th

installation and j th plot, and ε_{7b} represents the within tree error that is assumed to be $N(0, \sigma_{7b}^2)$. For western hemlock, only an installation random effect was estimated as only one plot was established at each installation.

2.2.3. Model fitting

Since annual parameters were desired but the observed variables were on longer growth intervals (1–15 years), the model formulation was altered using the technique of Cao (2000). The left side of the equation was the observed diameter or height growth of the tree during the observed growth period. The right side of the equation was a function which summed the estimated annual ΔDBH and ΔHT estimates from (3) and (7), respectively, over the number of growing seasons during the observed growth period using the updated parameter estimates from the GNLS or NLME optimization algorithms. For each growing season during the growth period, DBH and HT in (3) and (7), respectively, were subsequently updated, while UCR , SBA , BAL , and CCH were interpolated between their beginning values and ending values.

Initial parameter estimates were obtained using SAS v8.2 PROC MODEL assuming that SI , UCR , SBA , BAL , and CCH were constant during the period and errors were independent and homogeneous. Final equations were fitted using these initial parameter estimates and assuming SI was constant over time and UCR , SBA , BAL , and CCH changed linearly change during the growth period. Given the relatively short remeasurement period of most of the plots, i.e. 2–4 years, a linear change was deemed to be sufficient for this analysis. Further, preliminary analysis suggested little difference in the prediction bias achieved using different techniques for estimating the change in the independent variables.

Since these data violated the assumption of homogeneous variance, a power variance function of the initial diameter and crown ratio was incorporated into the fitting function for the diameter and height growth equations, respectively. The power variance function was common to all the plots and was defined in this analysis as $s^2(v) = |v|^{(2x)}$, where v is the variance covariate, $s^2(v)$ is the variance function evaluated at v , and x is the variance function coefficient. In addition, empirical evidence confirmed the diameter growth data only violated the assumption of independent errors, a continuous first-order autoregressive error structure as a function of period length was added to appropriately estimate parameter standard errors (Chi and Reinsel, 1989). GNLS and NLME were both fitted using the same procedures with regards to weighting and incorporation of an error structure and were fitted in SPLUS v6.2 using the NLME library which estimates the parameters via the maximum likelihood for both GNLS and NLME (Pinheiro and Bates, 2000).

Parameter estimates, variance functions, correlation structures, and random effects were evaluated using likelihood ratio tests at a significance level of 0.05 (Pinheiro and Bates, 2000). The final equations were evaluated by comparing residual standard error and coefficient of determination.

Following model fitting, the random coefficients were extracted for the installation level and were regressed on physiographic (longitude, latitude, elevation, slope, aspect), soil (depth, texture, rock content, water holding capacity), and mean climate variables (temperature, precipitation, vapor pressure deficit) to identify factors influencing the variability in growth. Slope and aspect were transformed using the suggestions of Stage (1976), while soil water holding capacity was estimated as outlined in Schwalm and Ek (2004). Mean climate variables were derived from daily weather records for a 23-year time period obtained from DAYMET (<http://www.daymet.org>).

2.3. Validation of Douglas-fir models

The annual diameter and height growth equations fitted for Douglas-fir were paired with previously developed individual tree static height to crown base (Hann et al., 2003) and annual mortality (Flewellling and Monserud, 2002) equations. Both the GNLS and NLME parameter estimates was used to predict 12–16 years of annual growth and mortality on the untreated plots on 12 SMC installations not used during model fitting. The installations were uniformly distributed through the western portion of the Pacific Northwest with initial breast-height age ranging from 23.5 to 46.5 years and site index ranged from 29.3 to 48.0 m at base age 50.

In addition, growth was also estimated using the NLME parameter estimates with a random installation effect predicted from physiographic, soil and mean climatic variables as described in the previous section. For comparison, the SMC variant of the individual tree distance independent growth model ORGANON version 8 (ORGANON v8; Hann, 2005) was also used to simulate growth on these plots. ORGANON uses a 5-year time step so linear interpolation was used to estimate growth for remeasurement periods that did not cover this time step. For comparison, estimates for bias and precision of the models were carried

out based on the following statistics:

$$MD = \frac{\sum (y_i - \hat{y}_i)}{n} \quad (8)$$

$$MD\% = \frac{\sum (y_i - \hat{y}_i)/y_i}{n} \times 100 \quad (9)$$

$$MSE = \frac{\sum (y_i - \hat{y}_i)^2}{n} \quad (10)$$

where MD is mean difference, MD% is mean percent difference, and MSE is mean square error.

3. Results

3.1. Diameter growth

A large range of tree sizes were available for the Douglas-fir and red alder diameter growth model, while the western hemlock data were more limited (Table 1). The models fit well with the fixed effects explaining between 66 and 88% of the original variation in the data. A likelihood ratio test indicated the random effects b_{3i} and b_{3j} were significant ($p < 0.0001$) for each of the three species (b_{3j} was not estimated for western hemlock). The NLME approach increased the fit index by 10–26% and reduced the residual standard error 15–52% when compared to fits obtained with GNLS. Weighted residuals showed no trends with explanatory variables.

The parameter estimates were consistent with biological expectations; that is, they were of the correct sign and approximate magnitude (Table 2). Diameter growth was a peaking function over initial diameter, increased with crown ratio and site index, and decreased with basal area in larger trees and stand basal area (Fig. 1). For a site index of 35.0 m and a basal area of $10 \text{ m}^2 \text{ ha}^{-1}$, diameter growth peaked at a diameter of 30.5, 25.0, and 14.8 cm for Douglas-fir, western hemlock, and red alder, respectively. The responses of western hemlock and red alder increased with increasing crown ratio ($\beta_{33} > 1.0$) whereas Douglas-fir's response decreased with increasing

Table 1
Description of the diameter growth rate data sets for Douglas-fir, western hemlock, and red alder trees

Variable	Douglas-fir		Western hemlock		Red alder	
	Mean	Range	Mean	Range	Mean	Range
Individual tree	$N = 57,074$		$N = 11,479$		$N = 46,546$	
DBH (cm)	10.7	0.1–97.5	6.2	0.1–35.1	5.9	0.1–28.2
UCR	0.75	0.10–0.99	0.96	0.47–0.99	0.73	0.1–0.99
BAL ($\text{m}^2 \text{ ha}^{-1}$)	10.4	0.0–178.0	3.9	0.0–36.9	4.7	0.0–25.9
Individual plot	$N = 356$		$N = 7$		$N = 132$	
SBA ($\text{m}^2 \text{ ha}^{-1}$)	16.8	4.0–178.2	6.2	2.0–37.0	6.8	0.5–26.0
Installations	$N = 210$		$N = 7$		$N = 30$	
BH AGE	12.3	0.1–60.4	15.4	6.1–33.6	8.5	3.0–20.0
SI (m at 50-year)	40.1	16.6–60.3	36.1	27.2–39.3	29.3	23.0–41.3
Length of growing period (years)	4.7	1–12	2.5	2–4	3.0	1–15

Variables are: diameter at breast height (DBH), uncompacted crown ratio (UCR), basal area in larger trees (BAL), stand basal area (SBA), breast height age (BH AGE), and site index (SI).

Table 2

Parameters and asymptotic standard errors for predicting the diameter growth rate (Eq. (3)) of untreated Douglas-fir, western hemlock, and red alder fitted using generalized nonlinear least squares (GNLS) and multi-level nonlinear mixed effects (NLME) procedures

Parameter/standard error	Generalized nonlinear least squares			Multi-level mixed effects		
	Douglas-fir	Western hemlock	Red alder	Douglas-fir	Western hemlock	Red alder
β_{30} (S.E.(β_{30}))	-3.6865 (0.0392)	-3.0984 (0.0479)	-3.6166 (0.0592)	-2.9553 (0.4009)	-2.3867 (0.8991)	-3.4805 (0.4566)
β_{31} (S.E.(β_{31}))	0.2121 (0.0081)	0.4617 (0.0059)	0.3847 (0.0125)	0.4222 (0.0063)	0.5818 (0.0076)	0.3953 (0.0065)
β_{32} (S.E.(β_{32}))	-0.00046 (0.00002)	-0.00032 (0.00001)	-0.0015 (0.00009)	-0.00005 (0.00002)	-0.00041 (0.00001)	-0.0008 (0.0003)
β_{33} (S.E.(β_{33}))	0.1878 (0.0202)	4.2445 (0.0767)	1.3000 (0.0179)	0.3488 (0.0219)	1.7334 (0.0650)	1.5890 (0.0249)
β_{34} (S.E.(β_{34}))	1.0778 (0.0098)	0.9399 (0.0144)	1.3619 (0.0276)	0.8932 (0.1052)	0.7173 (0.2507)	1.2685 (0.1402)
β_{35} (S.E.(β_{35}))	-0.0069 (0.00007)	-0.0010 (0.00003)	-0.0085 (0.0003)	-0.0036 (0.00005)	-0.0009 (0.00003)	-0.0022 (0.00007)
β_{36} (S.E.(β_{36}))	-0.1257 (0.0028)	-0.2488 (0.0021)	-0.2426 (0.0058)	-0.2873 (0.0041)	-0.3074 (0.0033)	-0.3926 (0.0043)
β_{37} (S.E.(β_{37}))	0.0145 (0.0043)	0.0099 (0.0041)	-0.0648 (0.0068)	0.0412 (0.0041)	-0.0452 (0.0053)	-0.0193 (0.0037)
S.E.(β_i)	-	-	-	0.0443	0.0389	0.0322
S.E.(β_j)	-	-	-	0.0038	-	0.0021
Fit index	0.88	0.86	0.66	0.97	0.95	0.83
Residual standard error	2.58	0.62	1.23	1.24	0.40	1.04

Fit index and residual standard error for each model are also given.

crown ratio ($\beta_{33} < 1.0$). Likewise, red alder diameter growth increased more rapidly with increasing site index ($\beta_{34} > 1.0$) than Douglas-fir and western hemlock which were more linear with site index. Douglas-fir exhibited a more pronounced response to larger trees or asymmetrical competition (β_{35}) followed by red alder then western hemlock (Table 2). When compared to Douglas-fir and western hemlock, the parameter estimate on SBA (β_{36}) for red alder suggested it was more responsive to stand density or symmetrical competition (Table 2).

3.2. Height growth

Similar to diameter growth, a large range of tree sizes were available for the Douglas-fir and red alder height growth model, while the western hemlock data were quite limited (Table 3). The parameter estimates were consistent with biological expectations (Table 4). The model fits were adequate as between 53 and 85% of the original variation was explained by the fixed effects. The random effects were significant for each of the species ($p < 0.0001$). NLME increased the fit index by 11–20% and decreased the residual standard error by 16–26% when compared to the GNLS fit. Weighted residuals showed no trends with explanatory variables.

For red alder and western hemlock, compacted crown ratio provided a significantly better fit than uncompact crown ratio. Uncompact crown ratio, however, was significantly better than compacted crown ratio for Douglas-fir. The asymptote (β_{70}) for western hemlock was not significantly different than one regardless of the estimation procedure, indicating that actual growth was similar to that projected by the dominant height growth equation (Fig. 2). In contrast, the asymptote was significantly less than one in alder and greater than one in Douglas-fir (Table 4), indicating that actual growth was lower and higher than expected by the dominant height growth equation, respectively. All species showed strong height growth responses to CR. Douglas-fir exhibited slow height growth below a CR of 0.3 and dramatically increased above. In contrast, red

alder and western hemlock were responsive across the range of CR. The pattern across CCH was strongly dependent on CR for western hemlock and red alder but not for Douglas-fir.

3.3. Analysis of random effects

3.3.1. Diameter growth

Regressing the installation random effects on physiographic features uncovered a few interesting relationships. The intercept of the Douglas-fir diameter growth equation showed a significant trend with annual precipitation (PRCP), elevation (ELEV), slope (%SLOPE), and aspect (Table 5). Parameter estimates suggested Douglas-fir diameter growth peaked on north-east facing slopes and at 220 cm of precipitation. The intercept of the red alder equation was related to elevation, slope, and aspect. The parameter estimates indicate that the red alder intercept tends to be highest on north-east facing areas. Western hemlock showed no significant relationship with any physiographic variables.

3.3.2. Height growth

The installation random effects for height growth were highly variable and provided fewer meaningful relationships with physiographic features than the diameter growth random effects. The Douglas-fir equation showed a significant relationship with slope, aspect, and percent rock content in the soil B horizon (%ROCK.B; Table 5). The parameter estimates indicated that asymptote of the height growth modifier was greatest on north-west facing sites. The asymptote of the red alder equation was related to slope, aspect, and elevation. The parameter estimates indicated that the asymptote was highest on east facing slopes. Western hemlock showed no significant relationship with any physiographic variables.

3.4. Validation of models and fitting technique

Mean difference, mean percent difference, and mean square error (MSE) for the three equations are given in Table 6. The

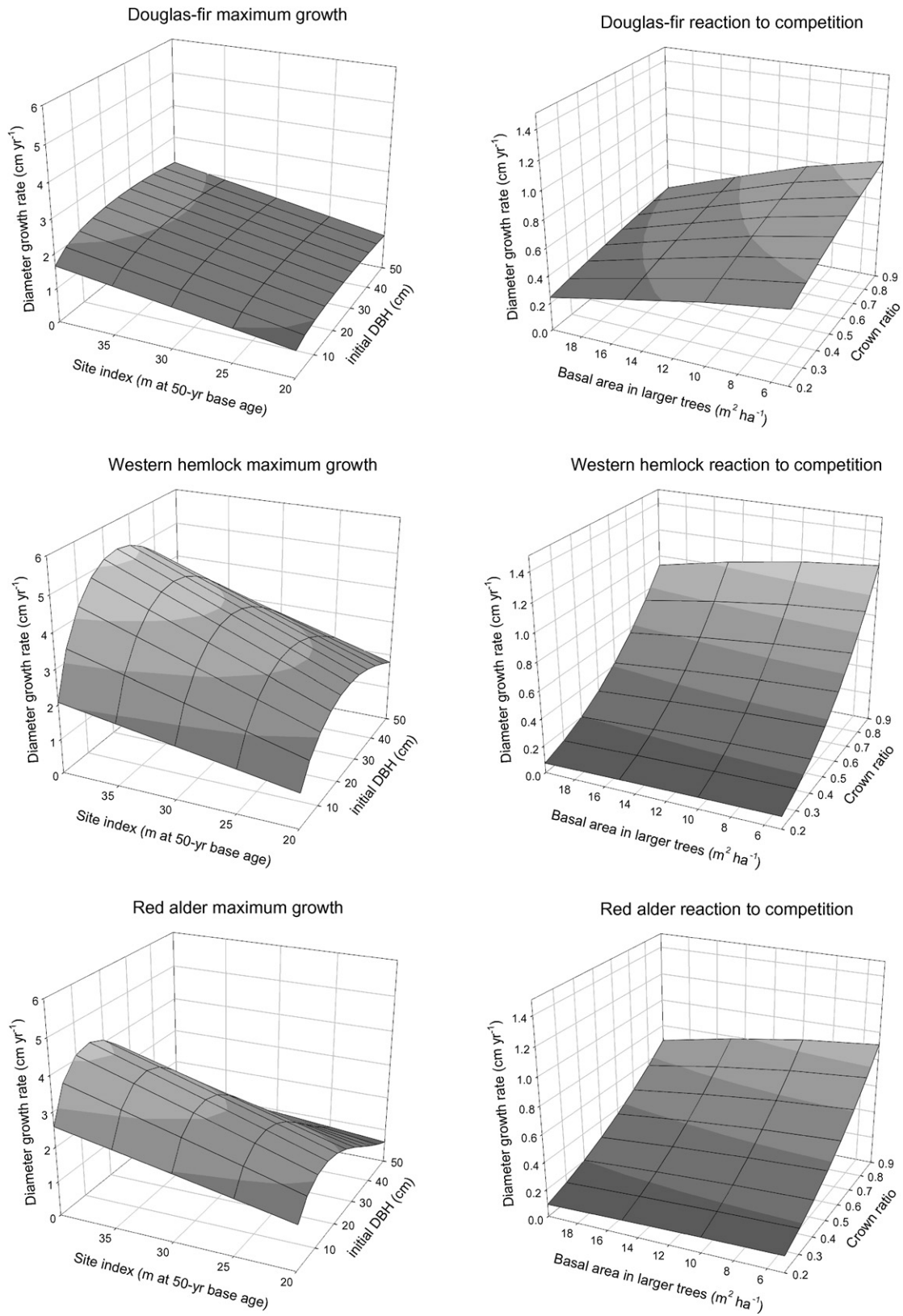


Fig. 1. Predicted surface response for annual diameter increment using Eq. (3) for an open-grown tree at varying levels of site index (left panel) and for an average size tree with increasing competition (right panel) by species.

Table 3

Description of the height growth rate data sets for Douglas-fir, western hemlock, and red alder trees

Variable	Douglas-fir		Western hemlock		Red alder	
	Mean	Range	Mean	Range	Mean	Range
Individual tree	<i>N</i> = 20,709		<i>N</i> = 8,077		<i>N</i> = 11,816	
DBH (cm)	14.7	0.2–97.5	5.4	0.1–33.8	5.6	0.1–28.2
HT (m)	10.83	0.50–52.48	4.95	0.20–20.72	6.18	0.20–22.60
CCH	7.9	0.0–303.5	6.0	0.0–207.3	31.16	0.0–464.1
UCR	0.77	0.1–0.99	0.97	0.49–0.99	0.78	0.1–0.99
Individual plot	<i>N</i> = 274		<i>N</i> = 7		<i>N</i> = 118	
SBA (m ² ha ⁻¹)	22.1	4.0–178.2	6.2	2.0–37.0	3.5	0.5–14.8
Installation	<i>N</i> = 210		<i>N</i> = 7		<i>N</i> = 30	
BH AGE	10.8	0.1–60.4	15.4	6.1–33.6	8.5	2.0–24.0
SI (m at 50-year)	39.7	16.6–60.3	36.1	27.2–39.3	29.3	23.0–41.3
Length of growing period (years)	3.8	1.0–12.0	2.2	2.0–4.0	3.0	1.0–15.0

Variables are: diameter at breast height (DBH), crown closure of the plot at the tip of the subject tree (CCH), uncompacted crown ratio (UCR), basal area in larger trees (BAL), stand basal area (SBA), breast height age (BH AGE), and site index (SI).

Table 4

Parameters and asymptotic standard errors for predicting the height growth rate (Eq. (7)) of untreated Douglas-fir, western hemlock, and red alder fitted using generalized nonlinear least squares (GNLS) and multi-level nonlinear mixed effects (NLME) procedures was made

Parameter/standard error	Generalized nonlinear least squares			Multi-level mixed effects		
	Douglas-fir	Western hemlock	Red alder	Douglas-fir	Western hemlock	Red alder
β_{70} (S.E. (β_{70}))	1.5673 (0.0065)	1.0033 (0.0060)	0.9286 (0.0067)	1.3020 (0.1643)	0.9880 (0.0282)	0.9415 (0.0230)
β_{71} (S.E. (β_{71}))	0.2928 (0.0085)	0.5722 (0.0298)	0.6176 (0.0411)	0.4794 (0.0388)	0.5501 (0.0238)	0.3833 (0.0816)
β_{72} (S.E. (β_{72}))	-0.00047 (0.00003)	-0.0125 (0.0019)	-0.0050 (0.0015)	-0.0018 (0.0008)	-0.0130 (0.0016)	-0.0075 (0.0063)
β_{73} (S.E. (β_{73}))	-0.0021 (0.00021)	-0.0015 (0.0002)	-0.0048 (0.0024)	0.0187 (0.0018)	-0.0040 (0.0016)	-0.0089 (0.0020)
β_{74} (S.E. (β_{74}))	6.0425 (0.2013)	5.2812 (0.4440)	4.1802 (0.8516)	2.7961 (0.3484)	6.4301 (0.4793)	2.9185 (0.6589)
β_{75} (S.E. (β_{75}))	0.0569 (0.0089)	0.0 (NA)	0.0418 (0.0298)	0.1126 (0.0126)	0.0 (NA)	0.0 (NA)
S.E. (β_i)	–	–	–	0.0139	0.1013	0.0144
S.E. (β_j)	–	–	–	0.0091	–	0.0068
Fit index	0.85	0.53	0.54	0.94	0.62	0.65
Residual standard error	1.04	0.82	1.14	0.77	0.69	0.96

Compacted crown ratio was used to estimate β_{74} for red alder and western hemlock, while uncompacted crown ratio was used for Douglas-fir.

equations fitted with NLME performed significantly better than the GNLS equations or NLME with predicted random effects. The NLME parameters reduced MSE by 13 and 21% for diameter and height growth prediction, respectively, when compared to the GNLS parameter estimate. There were some trends in the residuals using GNLS, while no obvious trends were present in the NLME simulations (Fig. 3). In comparison to a model with a longer time step, the biases achieved with the equations presented in this analysis were smaller than those produced by ORGANON. The NLME parameters reduced

MSE by 17 and 38% for diameter and height growth prediction, respectively, when compared against those produced by ORGANON.

4. Discussion

The procedure of Cao (2000) worked well for fitting annual diameter and height growth equations to hierarchical growth data representing varying growth period lengths. The technique avoided the need to linear interpolate during model fitting.

Table 5

Model, equation form, R^2 , and root mean square error (RMSE) for model predicting the influence of physiographic features on the random effects of each model

Model	Equation form	R^2	RMSE
Douglas-fir diameter growth	$-26.6559 + 0.3792 \times \ln(\text{ELEV}) + 0.4470 \times \text{ASP22} - 0.0260 \times \text{PRCP} + 5.6702 \times \ln(\text{PRCP})$	0.36	0.51
Douglas-fir height growth	$0.0301 + 0.0983 \times \text{ASP1} - 0.0018 \times \% \text{ROCK.B}$	0.07	0.14
Red alder diameter growth	$0.5138 + 0.3748 \times \text{ASP22} - 0.0896 \times \text{ELEV}$	0.29	0.12
Red alder height growth	$0.0844 - 0.0052 \times \% \text{SLOPE} + 0.0419 \times \text{COSA} - 0.3495 \times \text{ASP12}$	0.41	0.07

All parameter estimates were significant at $\alpha = 0.05$.

Elevation (ELEV, m); mean annual precipitation (PRCP, cm); percent rock content in the soil B horizon (%ROCK.B); percent slope (%SLOPE); cosine transformation of aspect (COSA, $[\cos(2\pi(\text{aspect}/360))]$); the percent slope multiplied by COSA (ASP1); cosine transformation of slope and aspect (ASP12, $[\% \text{SLOPE} \times \cos(4\pi(\text{aspect}/360))]$); and sine transformation of slope and aspect (ASP22, $[\% \text{SLOPE} \times \sin(4\pi(\text{aspect}/360))]$).

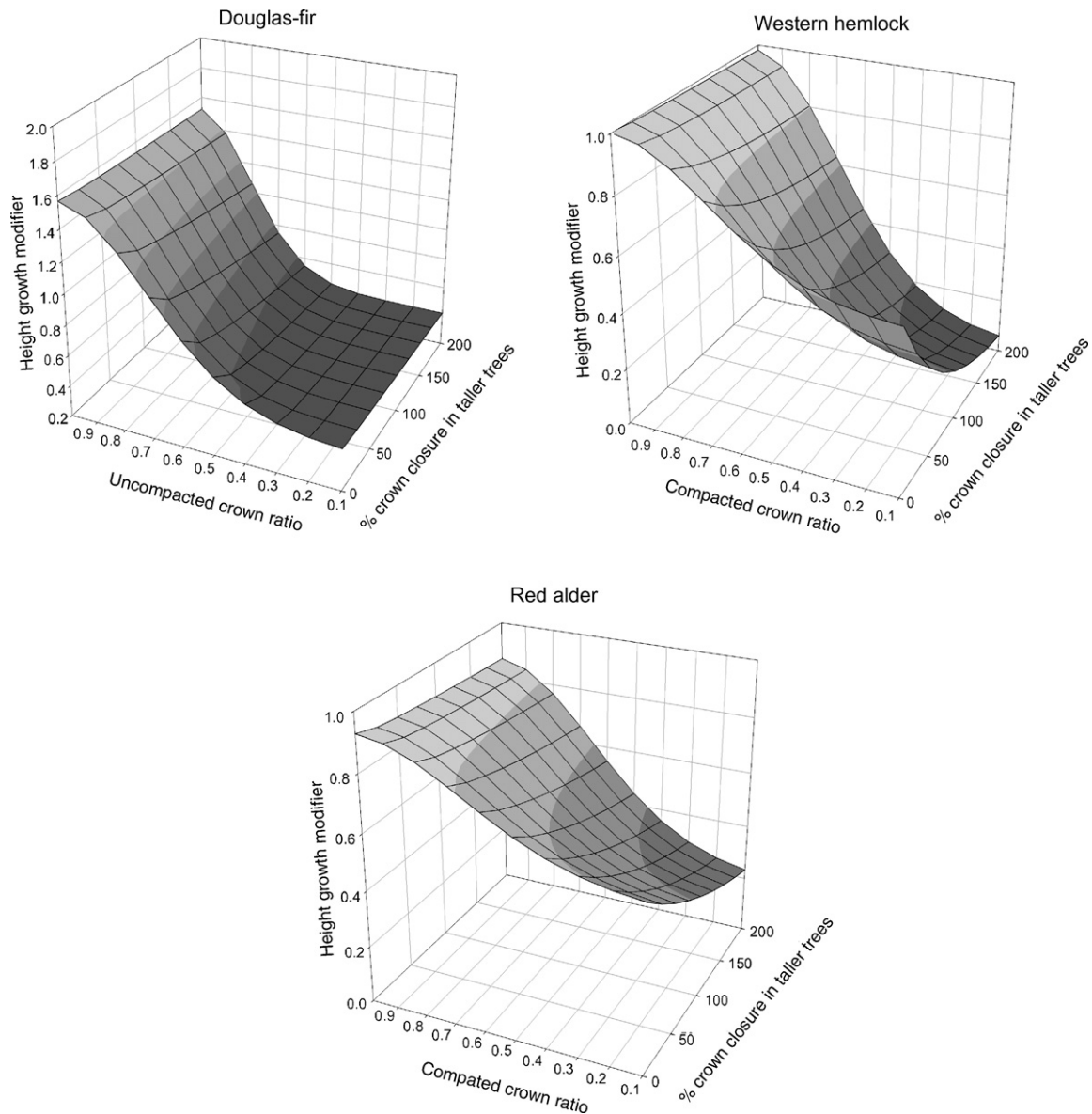


Fig. 2. Predicted surface response of the height growth modifier using Eq. (7) across a range of crown ratios and percent crown closure in taller trees for Douglas-fir, western hemlock, and red alder.

Further, the incorporation of correlation structure (GNLS) and random effects (NLME) were straight forward and resulted in reasonable parameter estimates. The Douglas-fir equations also demonstrated better performance on an independent data set than a currently used region growth model with a 5-year time step. These equations are also intended for future use in growth models, especially in light of the absence of such equations for red alder.

Unfortunately, there is little information on the performance of the fixed-effects parameter estimates from mixed models with regard to prediction. Some evidence suggests that height predictions from mixed effects height-diameter models using the best linear unbiased predictor techniques performed more poorly than regionally and locally developed models when extended to plots with no prior measurements (Monleon et al., 2004). Several recent growth equations have been parameterized using mixed-effects models with no assessment of their

performance on an independent dataset relative to ordinary least squares (e.g. Fahlvik et al., 2005; Nothdurft et al., 2006). This analysis indicated that diameter and height growth equations fitted with NLME procedures produced smaller bias and MSE values on an independent dataset than similar equations fitted with GNLS. This was especially true for the height growth model which is highly dependent on site index and the error associated with its estimation. The installation random effect on the modifier asymptote may account for some of this error possibly leading to better parameter estimates. An analogous process may occur when fitting the diameter growth model with a random intercept. Surprisingly, using the predicted random effect with the NLME models resulted in a bias that was between the NLME and GNLS models and the poorest MSE. Several possible reasons for this are poor parameterization of these installation effects equations, the effects are highly variable or have been diluted due to coarse

Table 6

Mean difference, mean percent difference, and mean square error for diameter at breast height (DBH; cm) and height (HT; m) after 12–16 years of simulation on 12 Stand Management Cooperative (SMC) control plots

Model	DBH (cm; $N = 1767$)			HT (m; $N = 472$)		
	Mean bias	Mean square error	% bias	Mean bias	Mean square error	% bias
GNLS	1.6479	2.4881	6.1035	1.2157	1.7256	4.0544
NLME	0.1102	2.1665	0.4508	-0.1993	1.3567	1.1695
NLME with predicted installation effect	1.2199	3.2797	5.1555	0.7156	2.0154	2.0503
ORGANON v8	-1.7883	2.6229	-7.0704	-1.4959	2.1820	-5.6759

Predictions were based on annual equations estimated by generalized nonlinear least squares (GNLS), multi-level nonlinear mixed effects (NLME), or the 5-year growth projections from ORGANON v8. In addition, annual growth was also predicted using the NLME parameter estimates with a predicted installation effect from the equations in Table 5. Initial breast height age of the plots was between 23.5 and 46.5 years, while site index ranged from 29.3 to 48.0 m at base age 50.

spatial or temporal resolution, or that there is a lack of causal relationships.

The diameter growth models presented for Douglas-fir and western hemlock and height growth models for Douglas-fir fit well and were generally consistent with observed growth patterns. The parameter estimates for Douglas-fir and, in part, western hemlock were consistent with those of Hann et al. (2003). The western hemlock equation presented here showed a significant effect of site index and the negative influence of predicted crown ratio not seen by Hann et al. (2003). Further, the equations highlighted some important ecological differences between species. Red alder is a shade intolerant hardwood, while Douglas-fir and western hemlock are

intermediate and very tolerant of shade conifers, respectively (Burns and Honkala, 1990). Thus as indicated by the equations presented in this analysis, red alder growth peaks early and is very sensitive to competition when compared to the other species.

The alder models and the height growth model for western hemlock did not result in fits as good as Douglas-fir. Two reasons were identified to explain this. First, the Douglas-fir data sets were fairly extensive, covering a wide range of growing conditions found in commercial plantations in the region. In contrast, the hemlock and alder data sets were less extensive and did not cover the larger, older end of plantation growing conditions. In particular, the current alder datasets

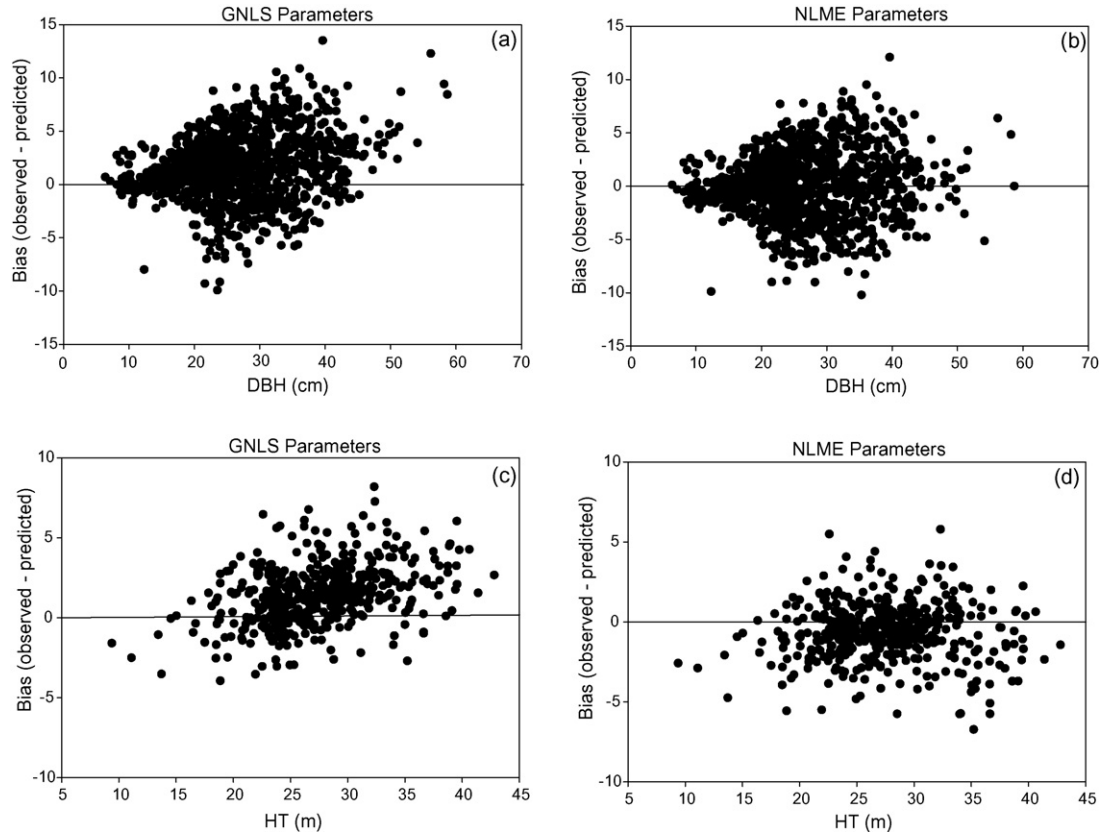


Fig. 3. Bias (observed — predicted) over observed diameter at breast height (DBH; cm) and total height (HT; m) after 12–16 years of simulation with the diameter and height growth equations fitted using generalized nonlinear least squares (GNLS; a, c) and multi-level nonlinear mixed effects (NLME; b, d) procedures on 12 Stand Management Cooperative installations not used during the fitting process.

have limited data from late in the stem exclusion stage of stand development (Oliver and Larson, 1996) where density-related effects appear. Second, Douglas-fir growth patterns are well-known and, hence, model forms are well-established. Model forms for other species have been borrowed from Douglas-fir, but, there is evidence that these forms may not be adequate for other species (Hann and Hanus, 2002; Hann et al., 2003). For example, stand density has been found to influence dominant height growth (Flewelling et al., 2001; Bluhm and Hibbs, 2006), but this was not accounted for in the dominant height growth curves used in this analysis. Several attempts were made to address this; however, the residuals showed no bias with stand density or other variables of importance. Regardless, these alder equations developed here are the first individual tree diameter and height growth models for plantation-grown red alder that have been published to our knowledge.

Random effects have been previously demonstrated to reduce the impact of autocorrelation in longitudinal forestry data: tree growth (Gregoire et al., 1995; Fang and Bailey, 2001), site index (Biging, 1985), stem profile (Gregoire and Schabenberger, 1996; Garber and Maguire, 2003), and branch architecture (Garber and Maguire, 2005). While random effects were successful in reducing the effect of autocorrelation in the height growth equations, they were not sufficient in accounting for the autocorrelation present within the diameter growth data. The addition of the first-order autoregressive process was necessary and successful at reducing the impact of autocorrelation in testing covariates. The combination of random effects and a continuous autoregressive process was also necessary in reducing the impact of autocorrelation in fitting taper equations in small plantation trees (Garber and Maguire, 2003). Although a poor model fit may be the cause of autocorrelation, the fits obtained in this analysis were quite good and other model forms did not perform any better.

Despite the poor performance of the predicted installations effects in the validation, an ancillary advantage of the mixed effects model approach was the ability to assess the variation in these effects across physiographic, soil, and climate factors. Nord-Larsen (2006) performed a similar type of analysis for European beech, but used indicator variables for each installation. These relationships were limited for Douglas-fir and red alder, while non-existent for western hemlock. The observed relationships suggested that diameter and height growth were significantly influenced by installation slope and aspect. These variables often showed a higher correlation with the random effects than actual climatic or soil variables. This is surprising because slope and aspect are commonly assumed to be proxies for climatic variables such as radiation and temperature. Douglas-fir and red alder showed the highest growth on north-facing aspects. The results for Douglas-fir are consistent with Hill et al. (1948) and McArdle et al. (1949) who also found north-facing slopes to be superior for productivity. Although the effects of soil water holding capacity (Hill et al., 1948) and parent material (Carmean, 1954; Steinbrenner, 1981) on height growth have also been reported for Douglas-fir in this region, no significant influence

of either factor was found in this analysis. The lack of a significant influence of physiographic effects on western hemlock growth is perplexing. This trend still occurs after the 7 plantation installations used in this analysis are combined with information from 48 other installations established in pure, natural stands. These results are in contrast to those of Steinbrenner (1981) who found trends in western hemlock dominant height growth to be adequately explained ($R^2 > 0.8$) by three variables, namely depth of the soil A horizon, soil texture, and elevation. The negative effects of increasing elevation and slope on red alder growth as well as growth being the slowest on south-facing aspects, however, were all similar with the results of Harrington (1986). Overall, physiographic variables were more powerful descriptors of variation in growth than soils or climate information, but this may be an artifact of using interpolated soils or climate data rather than site-specific measurements.

5. Conclusion

The technique presented by Cao (2000) fit with multi-level nonlinear mixed effects provided a good parameter estimation procedure for annualized equations for both a well-modeled (Douglas-fir) and lesser-modeled species (red alder) in the Pacific Northwest. It permitted the inclusion of larger and unmanipulated datasets for the development of diameter and height growth equations across a range of remeasurement periods. The inclusion of multi-level mixed effects improved the model fits, but the random effects had a limited relationship with physiographic features, mean climate, and soil properties. Compared to equations fitted without random effects, prediction biases on an independent dataset were, however, lowest for the multi-level mixed effect parameter estimates. Finally, annualized equations performed significantly better than a similar existing model (ORGANON v8) with longer time step. Thus, annualized equations are advantageous in that they provide a finer resolution of stand dynamics over time needed for the making decisions on the timing and degree of silvicultural intervention in high-intensity plantation forestry, but achieve a similar degree of bias as models with a longer time step. The finer temporal resolution of the annualized equations also allows for the assessment of annual climate variations on individual tree and stand growth dynamics, which can be effectively achieved by hybridization of these equations with a physiological model (e.g. Baldwin et al., 2001).

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