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Modeling regional and climatic variation of wood density and ring width in intensively managed Douglas-fir

Cosmin N. Filipescu, Eini C. Lowell, Ross Koppenaal, and Al K. Mitchell

Abstract: Characteristics of annual rings are reliable indicators of growth and wood quality in trees. The main objective of our study was to model the variation in annual ring attributes due to intensive silviculture and inherent regional differences in climate and site across a wide geographic range of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Ring specific gravity and ring width of Douglas-fir were examined at five long-term Levels-Of-Growing-Stock (LOGS) installations, three in the US and two in Canada, covering a latitudinal gradient between 43°N and 50°N. At each location, increment cores were collected from replicated plots with three levels of stocking: control (unthinned), lightly thinned (70% basal area retention), and heavily thinned (30% basal area retention). X-ray densitometry analysis provided ring specific gravity and width profiles for 5676 rings from 134 trees. The reduction of stand density through repeated entries resulted in decreased ring specific gravity and increased ring width. A four-parameter mixed-effects logistic model was used to predict ring specific gravity using cambial age, stand density (as number of stems per hectare), and two climatic variables: average temperature from March to May and total precipitation from April to August. A three-parameter mixed-effects logistic model was used to predict ring width using cambial age, stand density (as stand density index), and total climatic moisture deficit of June and July. Both models indicated significant site differences that were included in the models through indicator variables. Ring specific gravity increased slightly with increasing average temperature from March to May and decreasing total precipitation from April to August. Predictions of ring specific gravity of Douglas-fir appear to be more sensitive to changes in temperature compared with changes in precipitation.

Key words: Douglas-fir, specific gravity, annual ring width, thinning, wood quality.

Résumé : Les caractéristiques des cernes annuels sont des indices fiables de la croissance et de la qualité du bois chez les arbres. Le principal objectif de notre étude consistait à modéliser la variation des attributs des cernes annuels attribuable à la sylviculture intensive et aux différences régionales inhérentes au climat et aux stations sur une vaste étendue géographique occupée par le douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco). La densité et la largeur des cernes du douglas de Menzies ont été étudiées dans cinq endroits, trois aux États-Unis et deux au Canada, établis pour observer l'effet à long terme de la densité des tiges sur pied et couvrant un gradient latitudinal allant de 43° N à 50° N. À chaque endroit, des carottes ont été prélevées dans des placettes répliquées correspondant à trois niveaux de densité relative : témoin (pas d'éclaircie), éclaircie légère (rétention de 70 % de la surface terrière) et éclaircie forte (rétention de 30 % de la surface terrière). L'analyse par densitométrie aux rayons X a permis d'obtenir les profils de largeur et de densité de 5676 cernes provenant de 134 arbres. La réduction de la densité relative des peuplements par des interventions répétées a causé une diminution de la densité des cernes et une augmentation de la largeur des cernes. Un modèle logistique à effets mixtes à quatre paramètres a été utilisé pour prédire la densité des cernes annuels à partir de l'âge cambial, de la densité du peuplement (nombre de tiges à l'hectare) et de deux variables climatiques : la température moyenne du mois de mars au mois de mai et la précipitation totale du mois d'avril au mois d'août. Un modèle logistique à effets mixtes à trois paramètres a été utilisé pour prédire la largeur des cernes annuels à partir de l'âge cambial, de la densité du peuplement (indice de densité du peuplement) et du déficit hydrique total dû au climat en juin et juillet. Les deux modèles indiquaient qu'il y avait d'importantes différences entre les stations. Ces différences étaient incluses dans les modèles grâce à des variables indicatrices. La densité des cernes augmentait légèrement avec l'augmentation de la température moyenne du mois de mars au mois de mai et la diminution de la précipitation totale du mois d'avril au mois d'août. Les prédictions de la densité des cernes annuels du douglas de Menzies semblent plus sensibles aux variations de température qu'aux variations dans les précipitations. [Traduit par la Rédaction]

Mots-clés : douglas de Menzies, densité, largeur des cernes annuels, éclaircie, qualité du bois.

Introduction

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is one of the most valuable tree species grown in western North America. Its commercial importance lies in its use in structural applications because of its superior mechanical properties, i.e., strength and stiffness (Barrett and Kellogg 1989). Wood density is one of the most commonly used measures of wood quality in the forest products industry and an important indicator of mechanical properties (Jozsa et al. 1989; Bowyer et al. 2007). As a general rule, greater wood density is more suitable in applications where stiffness and strength are required (Bendtsen 1978), which includes markets for engineered products such as glulam timbers, plywood, and laminated veneers. Land management activities (e.g., thinning), often conducted to increase growth (and thus shift yield through space

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and time), can impact wood quality. There is a significant body of literature, often with conflicting results, related to thinning effects on ring specific gravity as summarized by Briggs and Smith (1986), Megraw (1986), Jozsa and Middleton (1994), and Bowyer et al. (2007). Many of these differences are attributed to factors such as growing conditions, site, initial stocking, and age at time of treatment (Larson et al. 2001). More recently, the role of wood density has emerged in carbon sequestration and biomass discussions (Kantavichai et al. 2010; Bontemps et al. 2013).

Environmental conditions, such as precipitation and temperature, also affect wood quality attributes (e.g., ring width and proportion of earlywood and latewood). Ring density and climate variable relationships have been reported on for a number of species (Brix 1972; Nicholls and Wright 1976; Robertson and Jozsa 1988; Franceschini et al. 2012). Climatic and regional variations in specific gravity of loblolly pine (*Pinus taeda* L.) were observed by Cregg et al. (1988) and Clark and Saucier (1989). Moreover, Splechtna et al. (2000) reported that the response of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) to climatic factors changed with elevation, which exhibited an inverse relationship with ring characteristics, such as ring width and density. However, latitudinal variation did not play a significant role in latewood proportion in black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) in research conducted by St-Germain and Krause (2008).

The latewood proportion within a growth ring strongly governs its wood density (Kubo and Jyodo 1996). Timing of the transition from earlywood to latewood is significant in determination of this proportion. Rossi et al. (2012) showed that successive phenological phases of xylogenesis from cell division to maturation are closely interconnected through complex cause and effect relationships. Antonova and Stasova (1997) noted that the transition from earlywood to latewood was significantly impacted by precipitation in larch (*Larix sibirica* Ledeb.). In addition, seasonal timing of water stress had an effect on latewood proportion in irrigated and fertilized young (23 years) Douglas-fir (Brix 1972). In older Douglas-fir trees (70 years) on Vancouver Island, the latewood width was found to relate to annual water deficit (Robertson et al. 1990). In the Pacific Northwest (PNW), less than 10% of the annual precipitation falls during the summer (Waring and Franklin 1979), and it is widely accepted that this seasonal lack of moisture is a major limiting factor of tree growth as soil moisture deficit generally occurs in the summer when high specific gravity latewood is being produced (Brix 1972). Lassen and Okkonen (1969), in studying the effects of rainfall and elevation in 50-year-old coastal Douglas-fir, found a negative linear trend of specific gravity with summer rainfall, independent of elevation. They also found specific gravity to be higher at lower elevations, which was attributed to higher proportions of latewood and thicker tracheid walls.

The role of temperature in wood density and latewood proportion has been studied in conjunction with other climatic factors. Cregg et al. (1988), working with loblolly pine, determined that low temperatures limited growth in the spring and high temperatures were limiting in the summer, while soil moisture availability played a role throughout the growing season. Schweingruber et al. (1978) found that the yearly maximum density in Swiss alpine trees directly correlated to temperature during the growing season and was also the most highly related single tree characteristic to climate data. In studying the effects of temperature and precipitation on the production of xylem cells in Scots pine (*Pinus sylvestris* L.), Antonova and Stasova (1993) found that temperature was the main influence on biomass accumulation in cell walls throughout the year.

Kantavichai et al. (2010) and Robertson et al. (1990) noted that studies have looked at precipitation, temperature, and soil but only for a limited number of species, and only a few considered the combined effects of these variables. Furthermore, the impact of long-term or repeated entries into a stand of trees has not been reported. The maturation of long-term field experiments (such as Levels-Of-Growing-Stock (LOGS)) provide an opportunity to use these research sites for further benefit to identify effects of intensive silviculture on wood quality attributes across a wide geographical range of Douglas-fir growing sites.

This study focused on quantifying the effects of repeated thinning regimes, climate, and site productivity on ring attributes (specific gravity and width) in Douglas-fir stands. Understanding the effects of management practices on wood quality, in addition to the influence of climatic factors, provides information on how best to match raw material to desired future objectives, whether that be carbon storage, biomass estimates, or wood products, and will enable improvements in the management and allocation of the forest resource.

Materials and methods

Site selection

The LOGS study was established in Oregon, Washington, and British Columbia to examine cumulative wood production, tree size development, and growing stock ratios in relation to eight thinning regimes and an unthinned control (Williamson and Staebler 1971). There were repeated entries into each stand and longer rotations than were reported in many other studies. These sites provide a wealth of historic measurement data (Curtis and Marshall 1986; Curtis et al. 1997) over a 40-plus year time frame. Nine LOGS installations were established between 1961 and 1970, representing different site classes (uniform throughout each installation) and origins (planted and natural), that include a large portion of the latitudinal range of coastal Douglas-fir. At each installation, there are three replications of eight thinning treatments plus untreated control plots for a total of twenty-seven 0.081-ha square plots. A detailed description of the study areas and experimental design can be found in Williamson and Staebler (1971).

Several of the original nine installations were not available for sampling, having been already harvested or damaged by wind. Five LOGS installations were selected for this study to cover the extent of the geographic range (northernmost to southernmost), as well as site quality, and different initial stand conditions (Table 1, Fig. 1). From the eight thinning treatments, two widely different thinning treatments, lightly thinned (70% basal area retention) and heavily thinned (30% basal area retention), were selected in addition to the unthinned control. These levels of retention were maintained through five repeated entries carried out following every 3 m of height growth of crop trees since the previous thinning. Three plot replicates of each of the three regime types (two thinning levels and control) were sampled at each installation for a total of 45 plots (nine plots × five locations).

Sample selection and X-ray densitometry

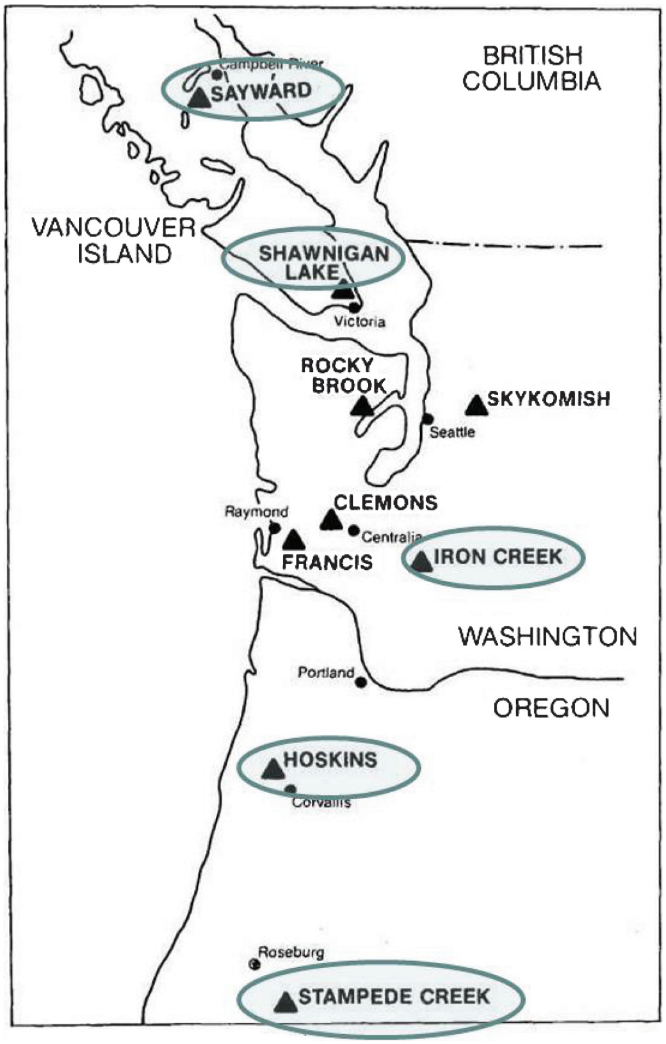
Distributions of diameter at breast height (DBH) in 5 cm classes for each of the 45 plots (five locations × three treatments × three replicates) were prepared from the most recent measurements. From each plot, 15 trees were selected based on stratified random sampling of weighted DBH distribution, with DBH remeasured in the field. These 15 trees were assessed using nondestructive tools and results will be presented in a subsequent report. When a dead sample tree was encountered, a substitute tree from the same diameter class was randomly selected as a replacement.

Increment cores were taken at breast height from a subsample of trees (three per plot) for X-ray densitometry measurements. These trees were randomly chosen from the highest weighted DBH classes of each of the 45 plots; these DBH classes differed with site and thinning treatment, with DBH ranging between 25 and 45 cm. In total, 135 trees were sampled (five locations × three treatments × three replicates × three trees). Increment cores (5 mm) were collected and kept frozen to prevent mold and stain. When it was time to process the cores, they were dried at 50 °C for

Table 1. Description of the study sites.

Site	Origin	Location (lat., long.)	Established	Age (years)	Site index (m at 50 years)	Elevation (m a.s.l.)	Annual temperature (°C)	Annual precipitation (mm)
Sayward	Planted	50°04′N, 125°35′W	1969	62	34	274	8.2	1401
Shawnigan Lake	Planted	48°38′N, 123°43′W	1970	64	29	335	8.9	1448
Iron Creek	Planted	46°24′N, 121°59′W	1966	60	40	762	8.5	2188
Hoskins	Natural	44°41′N, 123°30′W	1963	66	41	305	10.3	1816
Stampede Creek	Natural	42°53′N, 122°49′W	1968	75	34	823	9.8	1302

Fig. 1. Location of Levels-Of-Growing-Stock (LOGS) study sites. The locations used in the current study are highlighted.



24 h and then glued onto wood strips prior to sawing into radial strips (2 mm thick longitudinally). These were conditioned for at least 48 h to attain a uniform moisture content of 8%. One core sample was destroyed and lost during sample preparation in the lab, leaving 134 cores out of the 135 sampled trees.

Specific gravity (SG) profiles were generated from each sample with a linear resolution of 0.06 mm. The densitometer was calibrated to express SG on a green volume and oven-dried mass basis. Each sample profile included ring width, earlywood and latewood densities and proportions, ring densities, and total core density. Whole-ring specific gravity was calculated using the weighted areas of earlywood and latewood of each individual ring.

Stand and climate data

Plot-level data was available from the last published report (e.g., Curtis and Marshall 2009) for each installation and from the most recent measurement for all 45 plots (nine plots at each of the five locations). Number of trees, basal area, and quadratic mean diameter (qmd) were compiled for each plot at each remeasurement (between 8 and 10 successive historical data sets were available for each location), while linear interpolation was used to derive data for years between measurements. Stand density index (Reineke 1933) was also calculated at the plot level for every year since the establishment of each field installation.

Climate data were obtained for each site using ClimateWNA (Wang et al. 2012*b*). This climate model generates a suite of annual and monthly data based on latitude, longitude, and elevation. Mean monthly and annual temperature, and total monthly and annual precipitation and moisture deficit, were extracted for all five locations corresponding to each growth ring year.

Statistical analysis and model formulation

Preliminary analysis of ring SG on data from all samples revealed a sigmoid pattern with cambial age, where SG increases rapidly in rings closer to the pith, followed by a decline in the rate of increase and an asymptotic approach in rings farther from the pith (Fig. 2*a*). Several candidate equations were compared during the preliminary analysis, and a four-parameter logistic model was selected as most suitable to represent the SG profile. The four-parameter logistic model was used in previous studies of ring SG (Mora et al. 2007; Kantavichai et al. 2010). This model has the following form:

$$(1)\qquad f(\text{Age\_camb}, \beta) = \beta_0 + \frac{\beta_1 - \beta_0}{1 + e^{\left(\frac{\beta_2 - \text{Age\_camb}}{\beta_3}\right)}}$$

where Age_camb is the cambial age of the annual ring (also known as ring number from the pith), β_0 is the lower asymptote of SG in younger rings closer to the pith, β_1 is the upper asymptote of SG in older rings closer to bark, β_2 is the inflection point, and β_3 is the scale parameter.

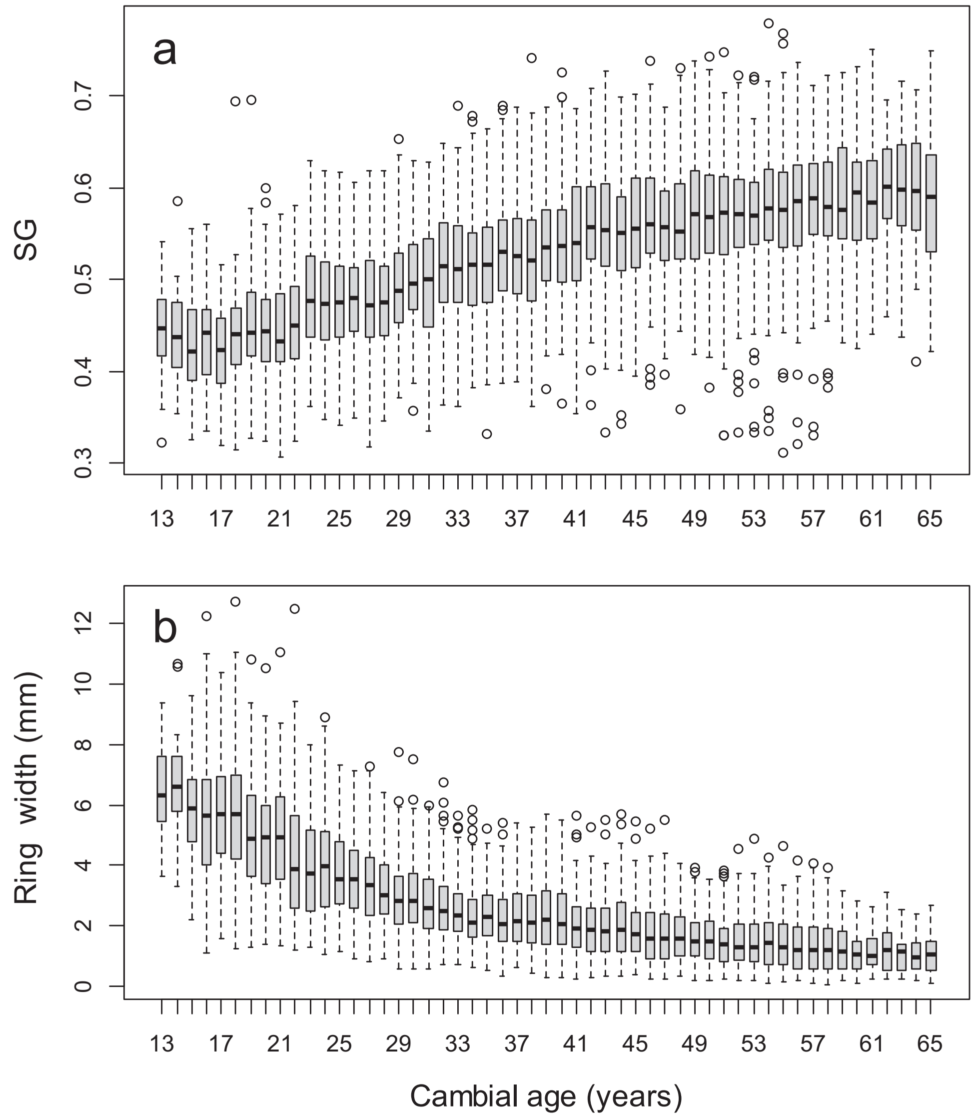
Profiles of ring width (Fig. 2*b*) revealed a monotonic decrease with cambial age, with an asymptotic approach in older rings. A three-parameter logistic function appeared the most suitable option after comparing several candidate functions. The model is

$$(2)\qquad f(\text{Age\_camb}, \beta) = \beta_0 + \frac{\beta_1}{1 + e^{(\beta_2 \times \text{Age\_camb})}}$$

where β_0 is the lower asymptote of ring width in older rings, β_1 is the initial parameter representing the width of rings closer to the pith, and β_2 is the scale parameter. Both the three- and four-parameter logistic models are parsimonious nonlinear functions that include parameters with biological interpretability.

Preliminary analysis also indicated the possibility of site differences for both ring attributes, SG and width. Since there was an interest in whether the northern sites differed from the southern

Fig. 2. Box plots of (*a*) ring specific gravity (SG) and (*b*) ring width (the box delineates the first and third quartile, the line within the box is the second quartile, and the whiskers represent the highest and lowest data as 1.5 times the box; outliers are data points beyond the 1.5 times interval).



sites, location was treated as a fixed level with indicator variables (1 if location, 0 otherwise) introduced in the models and tested for several combinations of parameters, whereas only the significant estimates were retained in the final model. The plots and trees were considered randomly sampled from the large populations; therefore, plot- and tree-level random effects were expressed in the model as $\mathbf{b}_i$ and $\mathbf{b}_{ij}$, where i = 1, …, 45 plots, and j = 1, …, 134 trees; both random effects were assumed to be normally distributed and centred at 0. The mixed effects parameters were modeled as

$$\beta_{ij} = \mathbf{A}_{ij}\boldsymbol{\beta} + \mathbf{B}_{ij,1}\mathbf{b}_i + \mathbf{B}_{ij,2}\mathbf{b}_{ij} \tag{3}$$

where $\boldsymbol{\beta}$ is the fixed-effects vector, $\mathbf{A}_{ij}$ is the fixed-effects design matrix, $\mathbf{b}_i$ and $\mathbf{b}_{ij}$ are the plot-and tree-level random-effects vectors, and $\mathbf{B}_{ij,1}$, $\mathbf{B}_{ij,2}$ are the corresponding random-effects design matrices.

In a first stage of modeling, all parameters were considered to have a random component; a diagonal structure of the variance–covariance matrices of the random effects were initially assumed to prevent issues owing to overparameterization. The number of random effects was reduced by dropping one random-effect term to obtain convergence and initial fit. Subsequently, restrictions on the variance–covariance matrices and error structures were relaxed, followed by testing the effects of possible covariates. Potential covariates included plot density (expressed as number of trees, basal area, qmd, and stand density index), as well as a large suite of combinations of annual and monthly climate variables (precipitation, temperature, and moisture deficit). Performance of nested models was compared using log-likelihood ratio tests and guided by the Akaike's information criterion (AIC). Once the covariates and the random-effects matrix structure were defined, the heteroscedasticity and serial correlation structure were identified to model the heterogeneity of variances and serial correlations between observations, respectively. Several candidates were explored for the variance function (power, exponential, and constant power) based on AIC reduction and distribution of residuals and for the serial correlation (autoregressive, moving average, and autoregressive – moving average structure) based on plots of the autocorrelation function (Pinherio and Bates 2000). All analysis was performed using maximum-likelihood modeling in the nlme package of R 2.15.0 (R Development Core Team 2012).

Table 2. Comparison of model performance with different covariates, random effects, and error structure for specific gravity.

Error structure	Covariates	AIC	BIC	logLik
Diag (b_0, b_1, b_2)		−21 742.5	−21 669.4	10 882.2
Unstr (b_0, b_1, b_2)		−21 772.1	−21 659.1	10 903.1
Unstr (b_0, b_1, b_2)	Indicator variable locations	−21 829.7	21 670.3	10 938.8
Unstr (b_0, b_1, b_2)	Indicator variable locations, N_{100}	−21 862.7	−21 696.6	10 956.3
Unstr (b_0, b_1, b_2)	Indicator variable locations, N_{100}, MA_{temp}, p_6	−21 872.5	−21 699.7	10 962.2
Unstr (b_0, b_1, b_2)	Indicator variable locations, N_{100}, t_{345}, p_{45678}	−21 892.5	−21 719.8	10 972.2
Unstr (b_1, b_2); AR(1)	Indicator variable locations, N_{100}, t_{345}, p_{45678}	−22 293.9	−22 174.3	11 164.9
Unstr (b_1, b_2); AR(2)	Indicator variable locations, N_{100}, t_{345}, p_{45678}	−22 314.6	−22 188.4	11 176.3
Unstr (b_1, b_2); AR(3)	Indicator variable locations, N_{100}, t_{345}, p_{45678}	−22 368.8	−22 235.9	11 204.4

Note: Diag, diagonal structure of the variance–covariance matrix (covariances are 0); Unstr, unstructured structure (i.e., with both variances and covariances); N_{100}, stand density (hundreds of trees per hectare); MA_{temp}, mean annual temperature; p_6, precipitation for June; t_{345}, average temperature from March to May; p_{45678}, total precipitation from April to August corresponding to the year the ring was produced; and AR(1), AR(2), and AR(3), autoregressive correlation structures of order 1, 2, and 3.

Results

Ring SG

Models with different combinations of random and fixed effects were evaluated. Fitting random effects for all four parameters was not possible therefore, one was dropped and the combination of three with the best fit was retained for further testing. A summary of the main steps in model selection is included in Table 2. Covariates that improved the fit the most were (1) indicator variables for location, (2) stand density (expressed as N_{100}, the number of hundreds of trees per hectare; the transformation was needed to match the size range of variables and facilitate parameter estimation), and (3) growing environment variables (temperature from March to May and precipitation from April to August). A variety of other growing-season variables were tested, with mean annual temperature and June precipitation also noted as good predictors, although both were inferior to the temperature from March to May and precipitation from April to August. Heteroscedasticity was not an issue that had to be addressed for the SG model and serial correlation was addressed by an AR(3) structure; one of the remaining random effects had to be dropped to accommodate the serial correlation structure, possibly because of overfitting issues. The final model for ring SG (Table 3) was

$$(4)\qquad y_{ijk} = \beta_0 + \frac{\beta_{1ij} - \beta_0}{1 + e^{\left(\frac{\beta_{2ij} - \text{Age\_camb}}{\beta_3}\right)}} + \varepsilon_{ijk}$$

$$\beta_0 = (\beta_0 + \beta_{01}\text{Ho})$$

$$\beta_{1ij} = (\beta_1 + \beta_{11}N_{100} + \beta_{12}t_{345} + b_i^{(1)} + b_{ij}^{(1)})$$

$$\beta_{2ij} = \left(\beta_2 + \beta_{21}\text{Sa} + \beta_{22}\text{Sh} + \beta_{23}p_{45678} + b_i^{(2)} + b_{ij}^{(2)}\right)$$

$$\varepsilon_{ijk} \sim (0, \sigma^2 R_{ij})$$

$$\sigma^2 R_{ij} = \sigma^2 \Gamma_{ij}(\phi)$$

$$\Gamma_{ij}(\phi) = \text{AR(3)}$$

$$\boldsymbol{b}_i = \left(b_i^1, b_i^2\right)^T$$

$$\boldsymbol{b}_{ij} = \left(b_{ij}^1, b_{ij}^2\right)^T$$

where k represents the annual ring; i = 1, …, 45 plots; j = 1, …, 134 trees; N_{100} is the number of trees (expressed in hundreds of trees per hectare) for each plot corresponding to the year of ring formation; t_{345} is the average temperature of March to May; p_{45678} is the total precipitation from April to August for the year the ring was produced; Ho, Sa, and Sh are indicator variables for locations Hoskins, Sayward, and Shawnigan (1 if location, 0 otherwise), Iron Creek was used as a reference; parameter β_3 is unrelated to the other variables and is treated as a fixed constant; random effects $\boldsymbol{b}_i$ and $\boldsymbol{b}_{ij}$ are represented by an unstructured matrix at plot i and tree ij; and $\Gamma_{ij}(\phi)$ is the serial correlation function.

Table 3. Parameter estimates, standard errors, p values, error-structure coefficients, and fit statistics for the final specific gravity model (eq. 4).

Parameter	Estimate	SE	p
β_0	0.3752	0.0081	<0.001
β_{01} (Ho)	0.0269	0.0067	<0.001
β_1	0.5427	0.0099	<0.001
β_{11} (N_{100})	0.0032	0.0007	<0.001
β_{12} (t_{345})	0.0026	0.0007	<0.001
β_2	31.5248	1.2695	<0.001
β_{21} (Sa)	−10.5089	1.7586	<0.001
β_{22} (Sh)	−11.4876	1.7584	<0.001
β_{23} (p_{45678})	0.0068	0.0013	<0.001
β_3	8.7013	0.5334	<0.001
Residual σ	0.0356		
φ_1	0.3691		
φ_2	0.0514		
φ_3	0.1157		
SD ($b_{i,1}$)	0.0357		
SD ($b_{i,2}$)	3.9821		
Cov ($b_{i,1}$, $b_{i,2}$)	0.683		
SD ($b_{ij,1}$)	0.0457		
SD ($b_{ij,2}$)	5.1999		
Cov ($b_{ij,1}$, $b_{ij,2}$)	0.356		
R^2 (fixed)	0.4799		
R^2 (fixed + random plot)	0.6127		
R^2 (fixed + random plot and tree)	0.8139		

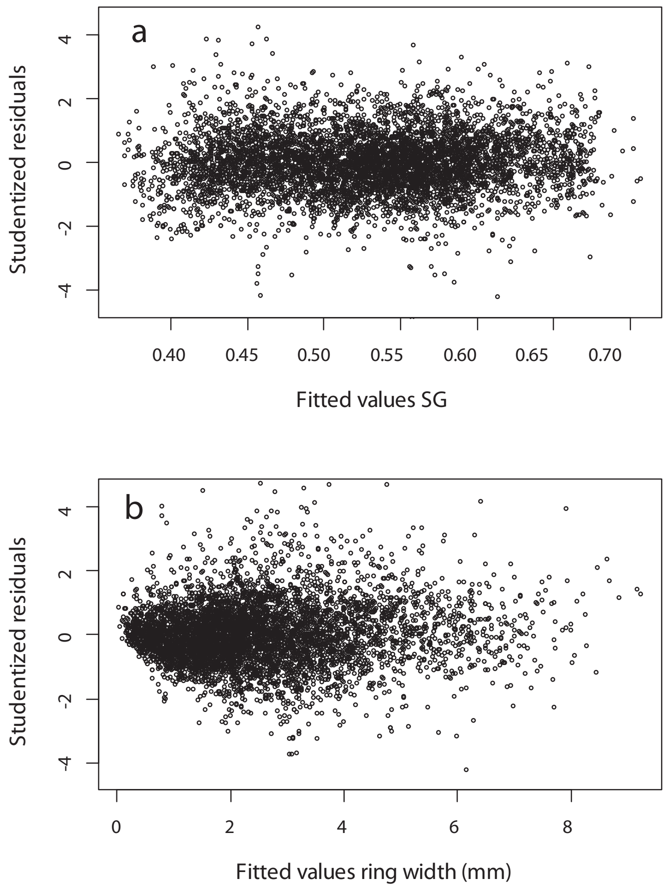
Note: Parameter labels (in parentheses) represent corresponding variables as per eq. 4; R^2 values are calculated based on the Pearson correlation between observed and predicted values. Ho, indicator variable for the Hoskins site; Sa, indicator variable for the Sayward site; and Sh, indicator variable for the Shawnigan site.

Plotting standardized residuals for the final SG model (Fig. 3*a*) validated the modeling assumptions and choice of model. Site differences (Table 3) were expressed by lower inflection points for Shawnigan and Sayward and a slightly higher low asymptote for Hoskins, while Stampede did not differ from the reference site (Iron Creek). These differences between locations (for control plots) are illustrated in Fig. 4*a*. In addition, stand density and average March to May temperature modified the upper asymptote, while precipitation from April to August affected the inflection point of the SG model. Within each location, the thinning regime led to a reduction in ring SG from the control (unthinned) to lightly and heavily thinned treatments (all sites indicated a similar pattern; an example is shown for Sayward in Fig. 5*a*).

Ring width

A similar fitting strategy was used for modeling ring width with a combination of fixed and random effects tested, followed by

Fig. 3. Distribution of standardized residuals for the final model of (*a*) specific gravity (SG) (eq. 4) and (*b*) ring width (eq. 5).

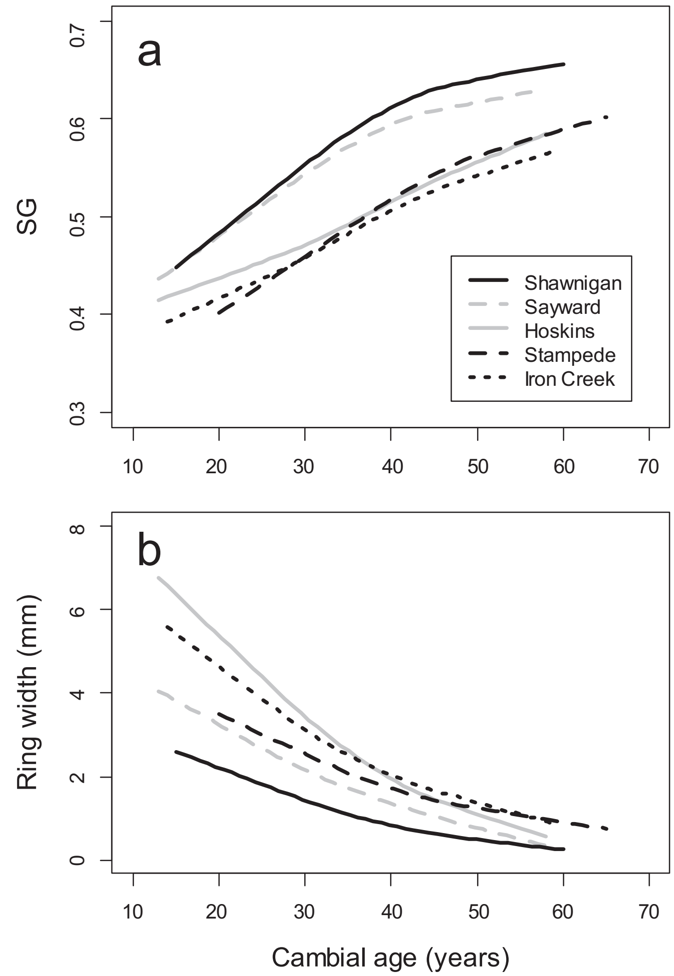


adding covariates, as well as including a function for unequal variance and a structure for serial correlation (Table 4). Covariates significant in the ring-width model were (1) the indicator variables for location, (2) the stand density (expressed as SDI_{100}, stand density index divided by 100) for each plot corresponding to the year of ring formation, and (3) the total moisture deficit for June and July. Surprisingly, none of the temperature variables were significant in the ring-width model, whereas growing-season precipitation was significant but provided an inferior fit. Heteroscedasticity was modeled by a power variance function of cambial age, and serial correlation was addressed by an MA(3) structure. The final model of ring width (Table 5) was

$$(5)\quad y_{ijk} = \beta_{0ij} + \frac{\beta_{1ij}}{1 + e^{(\beta_2 \times \text{Age\_camb})}} + \varepsilon_{ijk}$$
$$\beta_{0ij} = \left(\beta_0 + \beta_{01}\text{SDI}_{100} + \beta_{02}\text{md}_{67} + b_i^{(0)} + b_{ij}^{(0)}\right)$$
$$\beta_{1ij} = \left(\beta_1 + \beta_{12}\text{St} + \beta_{13}\text{Sa} + \beta_{14}\text{Sh} + b_i^{(1)} + b_{ij}^{(1)}\right)$$
$$\varepsilon_{ijk} \sim (0, \sigma^2 R_{ij})$$
$$\sigma^2 R_{ij} = \sigma^2 G_{ij}^{1/2}(\beta_{ij}, \delta)\Gamma_{ij}(\theta) G_{ij}^{1/2}(\beta_{ij}, \delta)$$
$$G_{ij}(\beta_{ij}, \delta) = \left|\text{Age\_camb}\right|^{\delta}$$
$$\Gamma_{ij}(\theta) = \text{MA}(3)$$
$$\boldsymbol{b}_i = \left(b_i^0, b_i^1\right)^T$$
$$\boldsymbol{b}_{ij} = \left(b_{ij}^0, b_{ij}^1\right)^T$$

where $i = 1, \ldots, 45$ plots, $j = 1, \ldots, 134$ trees; md_{67} is the cumulative climatic moisture deficit for June and July for the year the ring was produced; St, Sa, and Sh are the indicator variables for Stampede Creek, Sayward, and Shawnigan (1 if location, 0 otherwise), respectively, Iron Creek was used as a reference; parameter β_2 is unrelated to the other variables and is treated as a fixed constant; random effects $\boldsymbol{b}_i$ and $\boldsymbol{b}_{ij}$ are represented by an unstructured matrix at plot *i* and tree *ij*; $G_{ij}(\beta_{ij}, \delta)$ is the variance function, with δ the associated variance parameter; and $\Gamma_{ij}(\theta)$ is the serial correlation function.

Fig. 4. Predicted population mean trends of (*a*) specific gravity (SG) and (*b*) ring width for control (unthinned) at the five study locations.

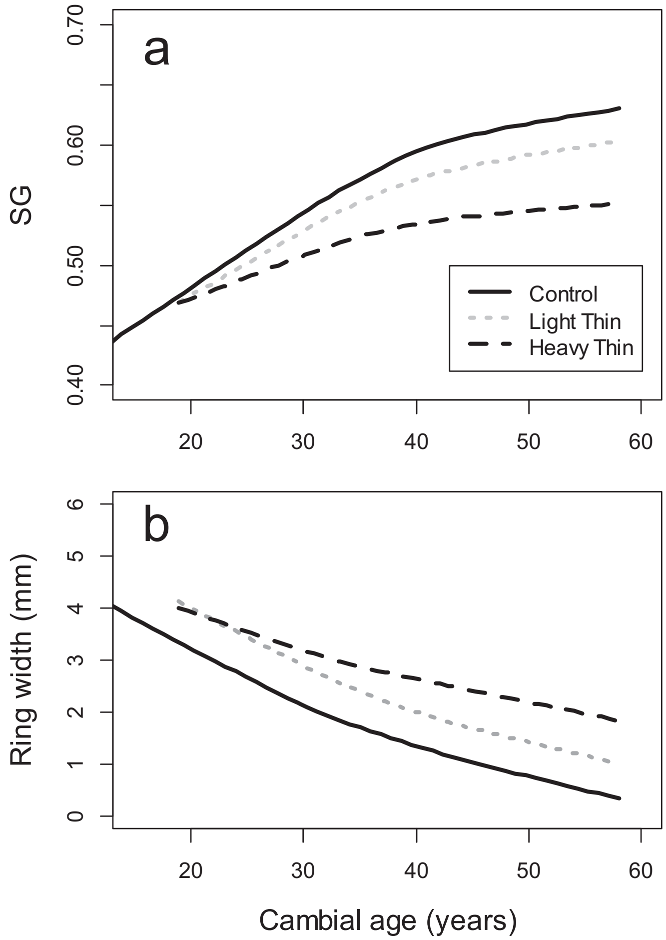


Plots of standardized residuals indicated no obvious residual trend in predicted ring width (Fig. 3*b*). Site differences (Table 5 and Fig. 4*b*) indicate lower initial parameters for Stampede Creek, Sayward, and Shawnigan (in descending order), whereas Hoskins did not differ significantly from the reference site (Iron Creek). The stand density index and moisture deficit of June and July both modified the lower asymptote of the ring-width model. The effect of stand density reduction on ring width was similar across all sites (an example is shown for Sayward in Fig. 5*b*).

Discussion

This study showed that models of Douglas-fir ring attributes (SG and width) vary significantly among geographical locations covering a large latitudinal and climatic gradient. To our knowledge, this is the first study reporting on regional differences in ring characteristics of Douglas-fir in the PNW. Regional variation in wood properties has been found by previous studies for other species such as loblolly pine (Tasissa and Burkhart 1998; Jordan et al. 2008; Antony et al. 2010) and radiata pine (*Pinus radiata* D. Don) (Palmer et al. 2013), with these differences mostly attributed

Fig. 5. Predicted population mean trends of (*a*) specific gravity (SG) and (*b*) ring width for the three thinning regimes at the Sayward location.



to physiographic variations in climate. Other tree characteristics, for example stem taper, have been found to be significantly affected by climate for lodgepole pine (*Pinus contorta* Douglas ex Loudon) in British Columbia (Nigh and Smith 2012). A much better understanding of the contributing factors and their interactions is required, especially considering a twofold projected increase in suitable growing habitat for Douglas-fir in British Columbia over the next several decades (Wang et al. 2012*a*). It is likely that other factors, such as site productivity and soil conditions, may also contribute to regionally contrasting ring properties in the PNW. Our results showed that there was an inverse relationship between site productivity and ring SG, whereas a direct relationship was observed between productivity and ring width. In the PNW, there is a gradient of soil conditions owing to soil parental materials, with soils developed on sedimentary deposits providing more favourable growing conditions compared with soils developed on igneous or glacial deposits (Littke et al. 2011).

The inverse relationship between growth rate and SG has been evaluated in numerous studies, although this relationship seems more pronounced for certain species such as those with a gradual transition between earlywood and latewood (Saranpää 2003). Wellwood (1952) reported that the wood density of second-growth stands of Douglas-fir was significantly lower on good sites compared with sites of average productivity, as well as for dominant trees compared with codominant and intermediate crown classes. Similar reductions in wood density with increased rate of growth have been observed for Douglas-fir trees released from suppression (Renninger et al. 2006) and following fertilization (Briggs et al. 1986) or thinning (Todaro and Macchioni 2011). However, the increased rate of growth following thinning does not always lead to lower SG. Jozsa and Brix (1989) and Kantavichai et al. (2010) showed that the SG of Douglas-fir may, in fact, increase after thinning on sites where soil moisture is a limiting factor, since thinning will lead to reduced moisture stress in the summer when latewood is being produced. On the other hand, Barger and Ffolliott (1976) found that thinning may also lead to increased formation of reaction wood that has increased SG but inferior physicomechanical properties.

Our results showed a tendency of lower SG for (1) earlier stages of stand development, (2) more productive sites, and (3) thinned plots (Figs. 4 and 5). These conditions are associated with higher rates of growth; however, faster growth rates may not always result in lower wood density because of other factors that may be involved. Live crown ratios (the length of live crown divided by total stem height) ranged between 30% and 40% for control unthinned, 45% and 50% for lightly thinned, and 60% to 70% for heavily thinned LOGS plots (Beddows 2002). At the same time, crown ratios tend to be higher in the earlier stages of stand development and also on the more productive Douglas-fir sites (Harrington et al. 2009). In addition, crown length affected other wood characteristics, such as strength and stiffness (Mason 2006; Kuprevicius et al. 2013). It seems that both crown size and stem proximity to crown may influence wood properties by regulating the rate of growth through the availability of photosynthates. It should be noted, however, that our models are based on samples collected at breast height, and crown impact will increase further with stem height position.

This study illustrates the importance of growing conditions on wood formation. Our SG model includes the average temperature from March to May and the total precipitation from April to August, whereas the ring width model includes the climatic moisture deficit during June and July. Our results confirm the findings of Kantavichai et al. (2010) who used the temperature from March to May but also the July moisture deficit in predicting ring SG of Douglas-fir on a dry site in the PNW. Moreover, Stoehr et al. (2009) showed that mean annual precipitation, as well as July precipitation and the temperature difference between the warmest and the coldest month, were variables that explained the variability of juvenile wood density in Douglas-fir. Different climate variables may result from differences between studies, such as site, sampling design, or stage of stand development. Factors other than just air temperature, precipitation, and soil moisture have causal effects on the physiology of growth and cambium phenology, such as light intensity or soil temperature (Dufour and Morin 2013).

The large within-ring differences in wood density between earlywood and latewood in Douglas-fir (Jozsa and Middleton 1994) can be explained by the different functions they perform for water transport. Wide tracheids with thinner walls in earlywood represent highly effective tissue with increased conductivity, whereas narrow tracheids with thicker walls in latewood are indicators of embolism resistance and water storage when water stress becomes prevalent in the summer (Domec and Gartner 2002). Kantavichai et al. (2010) argued that increased spring temperature may influence the earlywood to latewood ratio. In addition, we consider that higher spring temperatures may also lead to an increase in photosynthesis and carbon fixation. It is possible that these factors will influence growth phenology differently based on seed source and geographical location (Gould et al. 2012). In the southern range of Douglas-fir, an increase in annual temperature, which will bring warmer summers, may become a limiting factor through increased moisture deficit (Beedlow et al. 2013), while an increase in temperature may, in fact, improve growing conditions in the northern range of the PNW, similar to patterns reported for boreal species (Huang et al. 2013). However, our simulations indicate that a short-term increase in spring tem-

Table 4. Comparison of model performance with different covariates, random effects, and error structure for ring width.

Error structure	Covariates	AIC	BIC	logLik
Diag (b_0, b_1)		11 607.7	11 660.8	−5795.8
Unstr (b_0, b_1)		11 571.8	11 638.3	−5775.9
Unstr (b_0, b_1)	Indicator variable locations	11 524.2	11 610.6	−5749.1
Unstr (b_0, b_1)	Indicator variable locations, SDI_{100}	11 465.1	11 558.2	−5718.6
Unstr (b_0, b_1)	Indicator variable locations, SDI_{100}, An_{precip}	11 458.9	11 558.6	−5714.4
Unstr (b_0, b_1)	Indicator variable locations, SDI_{100}, md_{67}	11 436.7	11 536.4	−5703.4
Unstr (b_0, b_1); VarPower (~Age_camb)	Indicator variable locations, SDI_{100}, md_{67}	9867.8	9964.1	−4912.9
Unstr (b_0, b_1); VarPower (~Age_camb); MA(1)	Indicator variable locations, SDI_{100}, md_{67}	8310.5	8423.5	−4138.2
Unstr (b_0, b_1); VarPower (~Age_camb); MA(2)	Indicator variable locations, SDI_{100}, md_{67}	7821.9	7941.5	−3892.9
Unstr (b_0, b_1); VarPower (~Age_camb); MA(3)	Indicator variable locations, SDI_{100}, md_{67}	7611.5	7737.8	−3786.8

Note: Diag, diagonal structure of the variance–covariance matrix (covariances are 0); Unstr, unstructured structure (i.e., with both variances and covariances); Age_camb, cambial age of the annual ring; SDI_{100}, stand density index (hundreds of trees per hectare); An_{precip}, annual precipitation; md_{67}, cumulative moisture deficit for June and July corresponding to the year the ring was produced; MA(1), MA(2), and MA(3), moving-average correlation structures of the order 1, 2, and 3.

Table 5. Parameter estimates, standard errors, p values, error-structure coefficients, and fit statistics for the final ring width model (eq. 5).

Parameter	Estimate	SE	p
β_0	2.0414	0.1480	<0.001
β_{01} (SDI_{100})	−0.1219	0.0122	<0.001
β_{02} (md_{67})	−0.0007	0.0001	<0.001
β_1	18.8234	0.9710	<0.001
β_{12} (St)	−6.4792	1.1029	<0.001
β_{13} (Sa)	−8.5921	1.1063	<0.001
β_{14} (Sh)	−14.8151	1.1779	<0.001
β_2	0.0562	0.0016	<0.001
Residual σ	33.3074		
θ_1	0.5468		
θ_2	0.3571		
θ_3	0.2108		
α	−1.1437		
SD ($b_{i,0}$)	0.4264		
SD ($b_{i,1}$)	2.9837		
Cov ($b_{i,0}$, $b_{i,1}$)	−0.995		
SD ($b_{ij,0}$)	0.6805		
SD ($b_{ij,1}$)	5.4760		
Cov ($b_{ij,0}$, $b_{ij,1}$)	0.658		
R^2 (fixed)	0.6993		
R^2 (fixed + random plot)	0.7239		
R^2 (fixed + random plot and tree)	0.8589		

Note: Parameter labels (in parentheses) represent corresponding variables as per eq. 5; R^2 values are calculated based on the Pearson correlation between observed and predicted values. St, indicator variable for Stampede Creek; Sa, indicator variable for the Sayward site; and Sh, indicator variable for the Shawnigan site.

Table 6. Sensitivity analysis of specific gravity models at two study locations (maximum percentage change in the predicted values).

Location	Variable		
	N_{100}	t_{345}	p_{45678}
Sayward (40 years)	13	1.3	0.8
Sayward (50 years)	10.5	1.4	0.3
Stampede Creek (40 years)	6.5	1.5	1.9
Stampede Creek (50 years)	4.9	1.7	0.9

Note: Maximum percentage change was derived using eq. 4 as the difference between predicted specific gravity for the range of one variable while the other predictive variables were held constant at average values. t_{345}, average temperature from March to May; p_{45678}, total precipitation from April to August corresponding to the year the ring was produced; and N_{100}, stand density (hundreds of trees per hectare).

perature and a decrease in growing-season precipitation will lead to slight increases in SG for both southern and northern locations. Predictions seem to be more sensitive to changes in temperature compared with changes in precipitation, although changes induced by temperature and precipitation are much smaller relative to changes induced by the manipulation of stand density (Table 6). Furthermore, the inclusion of climate variables in our SG model seem to support recent findings that chronologies based on wood properties may be useful for climate studies in cases where tree-ring chronologies are not able to isolate the climate signal (Drew et al. 2013).

Our modelling approach relied on the use of mixed-effects hierarchical models. These tools are useful and flexible for analyzing longitudinal data, such as ring chronologies. The main advantages of these models are the ability to develop a unique variance–covariance structure and the ability to account for heteroscedasticity and serial correlations (Fang and Bailey 2001). Subject-specific predictions are conditional, however, on availability of previous subject data; such data may not be readily available, especially for ring SG; however, availability of nondestructive tools, such as those based on microdrill resistance, may provide data necessary for local calibration. Even in the absence of previous information, population-averaged predictions are entirely possible; R^2 values for fixed models of SG (0.47) and of ring width (0.69) indicate that population-level predictions are a viable option (Tables 3 and 5). The increase in goodness of fit for mixed-effects models accounting for plot- and tree-level random effects points to microsite and intertree variability.

Models developed in this study advance our understanding of processes and factors affecting ring properties in Douglas-fir. At the same time, these models can serve practical purposes for predictions of ring properties under various management regimes. Scenario simulations are becoming more and more possible based on the increased availability of data from models such as ClimateWNA coupled with traditional growth and yield models. For example, the influence of two planting densities on ring SG at different ages is illustrated for our southernmost and northernmost sites (Table 7). It is notable that SG differences between the two planting scenarios become less pronounced over time, in agreement with other studies reporting a lower correlation between growth rate and wood density with stand age (Koubaa et al. 2000). Furthermore, ring width constitutes one of the major criteria in the determination of log quality reflected by the British Columbia provincial scaling manual (Ministry of Forests, Lands, and Natural Resource Operations 2011). According to these grading rules, a Douglas-fir log can be categorized in the highest (and most valuable) grades for sawing or peeling if ring widths are lower than 3–4 mm. Such a requirement does not seem to be a problem at the two sites on Vancouver Island even in the highly thinned treatment, in contrast with the more productive southern sites where thinning may not be recommended if production of higher log grades is desired. Decisions such as how many trees to plant and whether or not to manipulate stand density further will become increasingly important for shorter rotations and will

Table 7. Estimated ring specific gravity over time for two planting scenarios at two study locations.

	Age (years)			
Scenario	30	40	50	60
Sayward				
Plant 2500 stems/ha	0.5393	0.5747	0.5866	0.5869
Plant 1100 stems/ha	0.5228	0.5611	0.5767	0.5809
Stampede Creek				
Plant 2500 stems/ha	0.4767	0.5320	0.5655	0.5775
Plant 1100 stems/ha	0.4654	0.5237	0.5604	0.5746

Note: t_{345}, average temperature from March to May; p_{45678}, total precipitation from April to August corresponding to the year the ring was produced. Values of ring specific gravity were derived using eq. 4, with multiyear normals of temperature and precipitation derived from the ClimateWNA model (for Sayward, t_{345} = 7.3 °C and p_{45678} = 270 mm; for Stampede Creek, t_{345} = 7.26 °C and p_{45678} = 227 mm) and stand density derived from the TASS-TIPSY model for Sayward and the CONIFERS and ORGANON models for Stampede Creek.

have multiple implications on both production (yield) and wood quality (juvenile core, knots, or wood density).

Future studies on regional variability of wood properties are required to broaden the applicability of results presented in this study. We used five long-term research locations covering a wide latitudinal gradient in the coastal range of Douglas-fir; therefore, it could be argued that our study only indicates a regional trend, whereas a greater number of sites and replication of sites within any given region will be required to further support our conclusions. Moreover, we detected significant differences among sites of different productivity; however, site productivity (i.e., site index) was not directly accounted for by our models and it may be blended with other site factors, such as elevation. While the study locations had different levels of productivity, the addition of sites across a wider range of site indices will further strengthen model predictions, as well as the inclusion of site index as an explicit predictive variable. Effective application of our models will also require validation against an independent data set.

Conclusion

This study assessed the impact of regional variability on ring SG and ring width for Douglas-fir at five long-term LOGS locations in the PNW. Stand density conditions and annual climatic variables were used to predict ring attributes. Ring SG decreased with reduction of stand density and increased site productivity, whereas ring width showed the opposite effect. Annual climatic variables (spring temperature and growing-season precipitation for SG and summer moisture deficit for ring width) explained additional variability in ring attributes. Management regimes can help achieve objectives and influence characteristics of the future crop through silvicultural prescriptions by better understanding and accounting for regional variation and environment conditions.

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