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Modeling knot geometry from branch angles in Douglas-fir (*Pseudotsuga menziesii*)

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Abstract

Lumber and veneer recovery from Douglas-fir (*Pseudotsuga menziesii*) trees depends on the size and distribution of knots. Two approaches have been used to simulate the effect of knots on recovery of these products: (1) prediction of recovery based on mill studies; and (2) simulated milling of virtual trees. A benefit of the latter approach is that different milling configurations may be tested. Knots in virtual logs are usually based on data from X-ray scanning. A novel approach was used in this study to model knot geometry by inferring the development of a branch knot over time from a chronosequence of branch angle and diameter measurements. Branch angle was modeled from a database of 17,953 branch measurements on 412 trees sampled in 16 Douglas-fir plantations. Branch angles from tree tip to crown base were assumed to represent a chronosequence describing the change in branch angle. Knot pith curvature was then derived from this chronosequence of branch angles and modeled as a first degree inverse polynomial, conditioned upon tree size and position within the tree bole. Knot pith curvature was predicted to follow a linear path near the tree tip, and became more curved with increasing age and depth into the crown.

Key Words

Knot geometry; Branch angle; Douglas-fir; Wood properties; Pith curvature

Introduction

Knots are one of the most important wood macroscopic features affecting product and value recovery from Douglas-fir (*Pseudotsuga menziesii*) trees. A knot is formed as a branch grows concurrently with, but generally perpendicular to the tree stem. The wood formed by knots creates discontinuities in longitudinal fibers of the tree bole, reducing wood strength (modulus of rupture), stiffness (modulus of elasticity) and visual appearance (Barbour and Parry 2001). A combination of these wood properties influences product recovery and value (Gartner 2005).

Over the last twenty years, numerous product recovery studies have been carried out in the Pacific Northwest (Fahey et al. 1991). These studies have generated product recovery equations that account for the effect of internal knots through surrogate variables like average branch size on the surface of the log. The possibility to link outputs from forest growth models to product recovery equations is well demonstrated (Briggs and Fight 1992; Houllier et al. 1995; Weiskittel et al. 2006). Simulation of tree growth and yield, using a system of forest growth and product recovery equations, assists in the selection of silvicultural treatments to maximize recovery of specific forest products.

Product recovery equations developed from mill studies depend on mill configuration and on the target products. As a result, these equations provide limited options for exploring alternative products and sawing patterns. A greater versatility for estimating product recovery can be achieved through simulated sawing of virtual logs (Mäkelä et al. 2010). In this approach, products are sawn from three-dimensional virtual logs produced from the outputs of a forest growth and yield model or X-ray scanner, and knot size and location is then evaluated along with

other features to grade the product. Numerous sawing simulators have been developed that vary widely with regard to computational sophistication and required input: SAWSIM (Halco 1970), BOF (Lewis 1985), AutoSaw (Todoroki 1990), RadSawSim (Ištvanic et al. 2010), Grasp (Occeña and Schmoldt 1995), LogCast (Occeña et al. 2000), TopSaw (Yun et al. 2008), Optitek (FPIInnovations 2014), WoodCim (Usenius 2000) and Cutlog (Turcan 2005). Analyses have demonstrated that simulated sawing can provide reliable estimates of product recovery (Todoroki et al. 2005).

A critical step in developing virtual Douglas-fir logs that can be passed from growth models into sawing simulators involves modeling the geometry of knots. The curvature in knot pith between stem pith and stem surface must be modeled accurately to represent the internal knot geometry within the bole and within sawn or peeled wood products (Figure 1). One of the first mathematical models for describing knot shape was developed for Scots pine (*Pinus sylvestris*) based on assumptions about cross-sectional shape and fixed angles (Samson 1993). Models allowing knot curvature were developed later from data collected on dissected knots in loblolly pine (*Pinus taeda*) (Trincado and Burkhart 2008), and Norway spruce (*Picea abies*) (Lemieux et al. 1997). Dissection techniques have increasingly been replaced by X-ray computed tomography (CT). This technique has been used to model knot geometry of Scots pine (Moberg 2006), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*) (Duchateau et al. 2013), Norway spruce (Andreu and Rinnhofer 2003; Oja 2000; Moberg 2001) and white spruce (*Picea glauca*) (Tong et al. 2013).

Curvature of the knot pith results from a gradual increase in branch angle (*VBA*) toward a horizontal position (branch angle throughout this analysis refers to angle of origin or angle at point of attachment to the main stem, measured relative to vertical). The angle of a branch formed at the tip of the tree tip defines the initial angle of the knot that eventually results from that branch. Curvature in the knot pith between the bole pith and stem surface (Figure 1) therefore reflects the change in branch angle over time. This time-series of branch angles can be observed in the chronosequence of branch angles from the tree tip to crown base. Inferring a true time-series of branch angles from the chronosequence of branches with increasing age and depth into crown offers a non-destructive sampling approach to construct a database for modeling knot pith curvature. The resulting model assumes that the angle chronosequence over older and deeper branches closely resembles the angle time series as a single branch ages. While quite reasonable from casual observation, the accuracy of this working hypothesis requires testing or validation with data not currently available.

The ultimate goal of this research was to develop a three-dimensional model for knots within Douglas-fir trees in the Pacific Northwest, so that knot size and location can be projected within virtual logs for sawing simulation. The specific objective of this study was to model the curvature of knots by analyzing a chronosequence of branch angles on standing trees. An assessment of mechanisms controlling knot formation, identification of analytical gaps, and future research needs are also discussed.

Methods

Field Data

The data used to fit the models for branch angle were first described by Roeh and Maguire (1997) and involved climbing the sample tree and placing a clinometer at the base of whorl branches and reading the angle to the nearest degree from the external scale. The database included 17,953 branch measurements (Table 2) taken from 412 trees (Table 3) across 16 Stand Management Cooperative (SMC) Type I and Type II installations (Maguire et al. 1991). The SMC installations are a network of experimental research plots in managed Douglas-fir forests, covering different levels of initial planting density, site class, and silvicultural treatments that include respacing, thinning, and fertilization.

Modeling database

Construction of a database for modeling knot pith curvature using a chronosequence of branch angles requires two precursor models: 1) a model accounting for the change in branch angle with depth into crown; and 2) a model for estimating diameter inside bark (*dib*) at any height on the tree bole. Equipped with these models, a suitable database for modeling knot pith curvature can be assembled as a time-series of Cartesian coordinates (x - y) representing the succession of points where the knot pith emerged from the cambial surface at the end of each growing season (Figure 2). The x -coordinates correspond to the horizontal distance to the bole pith (*rib*) and the y -coordinates correspond to the height of knot pith at cambial emergence (h_1).

A set of segmented polynomial taper models were available for estimation of *dib* at any height on a Douglas-fir stem (Walters and Hann 1986). Several models for branch angle (*VBA*) have been presented in the forestry literature (Table 1), including those for Sitka spruce (*Picea sitchensis*) (Cochrane and Ford 1978), Norway spruce (Colin and Houllier 1992), Douglas-fir

(Roeh and Maguire 1997; Weiskittel et al. 2007a), and Scots pine (Mäkinen and Colin 1998). However, some refinement of the model for Douglas-fir was deemed desirable.

Models for Douglas-fir branch angle

Two models were developed to predict the insertion angle of live branches from the top to bottom of individual Douglas-fir crowns. Best-subsets regression (regsubsets; leaps package; Lumley 2009) in the R statistical programming language (R Core Team 2015) was used to screen several linearized candidate models and associated explanatory variables. The proposed models are similar to existing equations (Roeh and Maguire 1997; Weiskittel et al. 2007a), with the first taking the following form:

$$[1] \quad VBA = (\omega_0 + \omega_{11}CR) + \omega_{12} \left[1 - e^{\left(\beta_{11}DINCR + \beta_{12}CL + \beta_{13}\frac{DBH}{HT} \right)} \right] + \varepsilon_1$$

where *VBA* was branch angle (insertion angle measured from vertical in degrees), ω_0 was an empirical minimum value calculated as the upper limit of the 25th percentile of minimum *VBA* observations for each tree in the modeling database, ω_{11} - ω_{12} and β_{11} - β_{13} were parameters to be estimated from the data, *DINC* was depth into crown from the tree top (m), *CL* was live crown length (m), *DINCR* was relative depth into crown (*DINC/CL*), *DBH* was tree diameter at breast height (cm), *HT* was total tree height (m), *CR* was live crown ratio (*CL/HT*), and ε_1 was the error term with $\varepsilon_1 \sim N(0, \sigma_{\varepsilon_1}^2)$. The empirically derived minimum value (ω_0) prevented the model from adverse effects of extremely low values of *VBA* that were attributable to damaged or malformed branches.

The second model for predicting branch angle allowed a more gradual increase in branch angle with increasing *DINCR* by including an effect of branch diameter (*BD*):

$$[2] \quad VBA = (\omega_0 + \omega_{21}CR) + \omega_{22} \left[1 - e^{(\beta_{21}DINCR + \beta_{22}CL + \beta_{23}DBH + \beta_{24}BD)} \right] + \varepsilon_2$$

where ω_{21} - ω_{22} and β_{21} - β_{24} were parameters to be estimated from the data, *BD* was the measured branch diameter (mm), ε_2 was the error term with $\varepsilon_2 \sim N(0, \sigma_{\varepsilon_2}^2)$, and all other variables were defined above.

Validation of branch angle models

Prior to fitting Equation [1] and Equation [2], a validation dataset was constructed. The validation dataset consisted of 3,281 branch measurements from 14 randomly selected SMC plots. The validation dataset represented about 16% of the entire dataset available for modeling, and both SMC Type I and II installations were represented. The means of the following statistics were computed to validate the branch angle models:

D = deviation = observed *VBA* – predicted *VBA*

AD = absolute deviation = |deviation|

D^2 = squared deviation = deviation²

Construction of a dataset for modeling knot pith curvature

No attempt was made in this analysis to account for the azimuth of the branch around the circumference of the stem. Until evidence accumulates to the contrary, branch distribution will be assumed to follow a uniform distribution around the stem, as has been found in intensively managed *Pinus taeda* plantations (Doruska and Burkhart 1994). Annual *x-y* coordinates were estimated for an average branch at each whorl of each tree sampled to construct the modeling

dataset. This process required the following three steps: (1) reconstruction of the stem *dib* profile for each year of past tree growth; (2) prediction of branch angle for each year the branch was alive (Equation 1); and (3) numerical solution of these equations to find the *x-y* coordinates of the intersection of stem *dib* profile and knot pith, corresponding to the point of knot pith emergence from the cambium (Figure 2).

The past *dib* of each tree was estimated from a segmented polynomial taper equation (Walters and Hann 1986). Estimation of past-annual *dib* profiles from the taper equation required reconstruction of past-annual *DBH*, *HT*, and *CL*. The past-annual *DBH* and *HT* were estimated using a scaling factor, which was the ratio of the current diameter and height to maximum potential diameter and height, for each year of reconstruction. Curves representing cumulative potential diameter growth were estimated using an annualized Douglas-fir *DBH* growth equation (Weiskittel et al. 2007b) that depended on only initial *DBH* and site quality (*SI*). Potential cumulative height growth curves were similarly estimated from a top-height growth equation (King 1966), and rescaled to individual sample trees using the ratio of current tree height to potential top-height for the respective site quality (*SI*) and tree age. These adjustments of the cumulative *HT* and *DBH* growth curves assumed past *DBH* and *HT* growth of any given tree had maintained the same proportion of maximum throughout the life of the sample tree.

A static allometric equation was developed to estimate height to crown base (*HCB*) for any year of backdating based on site quality and estimates of that year's *DBH* and *HT*. This estimate of *HCB* was used in the taper equation to estimate past *dib* profile, but also to identify the year of branch mortality. The *HCB* model was fit by combining eight different datasets from studies

with consistent definitions of *HCB* (i.e., consistent with “compacted crown ratio” *sensu* Monleon et al. (2004)). Three of the datasets were from experimental studies of young plantations at five separate locations in western Oregon and Washington, and included tree height and crown base height measurement from time of planting up to ten years of age (Maguire et al. 2009). Three of the datasets included SMC Type I, II, and III plots with measurements from more than 66 locations extending from southern Oregon to northern Vancouver Island, and with ages ranging from 4 - 58 years (Maguire et al. 1991). The final two datasets were from long-term studies at five different locations in Oregon and Washington, and included trees ranging in age from 37 - 92 years (Ares et al. 2007; Curtis et al. 1997). After testing several candidate models, the following equation was selected:

$$[3] \quad HCB = \frac{HT}{1 + \exp\left[\alpha_0 + \alpha_1 HT + \alpha_2 \left(\frac{HT}{DBH}\right) + \alpha_3 SI\right]} + \varepsilon_3$$

where, *HCB* was height to crown base (m), $\alpha_0 - \alpha_3$ were parameters to be estimated from the data, *SI* was King’s (1966) site index (m at 50-year breast height age), ε_3 was the error term with $\varepsilon_3 \sim N(0, \sigma_{\varepsilon_3}^2)$, and all other variables were defined above.

For each whorl on each tree, a time-series of branch angles (*VBA*) was predicted starting at the initial whorl height indicated by predicted cumulative tree height growth. After the crown base receded past a given whorl (implying branch mortality), the branch angles in the subsequent part of the time-series for that branch were fixed at the last angle predicted while the branch was still alive.

Models for knot pith curvature

Two models for estimating knot pith curvature were fit using the database of x - y coordinates of annual knot pith locations. These models were formulated based upon two potential applications requiring a slightly different set of predictor variables. The first and presumably dominant application was to estimate knot pith curvature during simulation of individual tree growth. In this application, tree level predictors such as DBH , HT , CL and whorl height (height of knot pith origin, h_0) would be available. Several model forms were tested, including a modified Weibull form (Duchateau et al. 2013) and a non-linear form that was a ratio of polynomials of radial distance (Lemieux et al. 1997). The final model was the following first-degree inverse polynomial, selected on the basis of model residual pattern (homogeneity of variance and lack of bias) and expected biological behavior:

$$[4] \quad H_{rib} = \frac{rib}{\left(\gamma_{10} + \gamma_{11}CL + \gamma_{12}\left(\frac{DBH}{HT}\right)\right) + rib\left(\gamma_{13} + \gamma_{14}rib_0 + \gamma_{15}\left(\frac{h_0}{HT}\right)\right)} + \varepsilon_4$$

where H_{rib} was the height of the knot pith above its estimated point of origin at the bole pith (cm), h_0 was the simulated whorl height where knot pith was defined to emerge from the bole pith (m), rib_0 was the radius inside bark at height h_0 (cm), rib was the radius inside bark at H_{rib} (cm), $\gamma_{10} - \gamma_{15}$ were parameters to be estimated from the data, ε_4 was the error term with $\varepsilon_4 \sim N(0, \sigma_{\varepsilon_4}^2)$, and all other variables were defined above.

The second model was developed for instances where only exterior features of the tree, including the height of branch attachment (h_l , BR_{ht}) are available. The final model for this application was the following first-degree inverse polynomial:

$$[5] \quad H_{rib} = \frac{rib}{\left(\gamma_{20} + \gamma_{21}CL + \gamma_{22}\left(\frac{DBH}{HT}\right)\right) + rib\left(\gamma_{23} + \gamma_{24}rib_1 + \gamma_{25}\left(\frac{h_1}{HT}\right)\right)} + \varepsilon_5$$

where H_{rib} was the height of the knot pith above its estimated point of origin at the bole pith, h_l was the height of knot pith at emergence from the cambium, rib_l was the radius inside bark at h_l , $\gamma_{20} - \gamma_{25}$ were parameters to be estimated from the data, ε_5 was the error term with $\varepsilon_5 \sim N(0, \sigma_{\varepsilon_5}^2)$, and all other variables were defined above.

The use of the pith curvature models was demonstrated by constructing some three-dimensional knots of the type that would be contained in a virtual tree or log for sawing simulation. Equation [5] was first applied to a tree typical of the Roeh and Maguire (1997) dataset ($DBH = 26$ cm, $HT = 16$ m, $CL = 14$ m) to predict the pith or central axis of several branches at different heights within the live crown. The knot diameter at the point of branch insertion was assumed circular and symmetric around the knot pith and equal to the predicted maximum branch diameter (BD_{max}) at a specific depth into crown (Weiskittel et al. 2007a). The diameter of the knot was assumed to decrease non-linearly as radial distance (rib) approached zero in a manner described by the following equation:

$$[6] \quad KD = BD_{max} \left[\frac{1 - e^{(-\delta \cdot rib)}}{1 - e^{(-\delta \cdot rib_{max})}} \right]$$

where KD was the knot diameter at rib (cm), BD_{max} was the predicted maximum branch diameter at the point of insertion (cm), δ was a subjectively estimated shape parameter, and rib was radial distance from the tree bole pith (cm).

Results

Equations [1] and [2] explained 16.6% and 21.5%, of the variation (R^2) in branch angle, respectively (Table 4). The residuals for both equations indicated constant variance across the

range of predicted branch angles and depth into crown (Figure 3). Predictions from Equations [1] and [2] indicated that branch angle increased consistently with depth into crown for branches on individual Douglas-fir trees (Figure 4). The trend in branch angle varied by the combination of *DBH*, *HT*, and *CL* among individual trees. Large trees and those in a superior social position tended to have a greater initial branch angle, but converged toward the same maximum branch angle at crown base as smaller trees (Figure 5). Equation [2] produced a behavior very similar to Equation [1], but caused the branch angle to change at a slower rate with increasing *DINC*. Instabilities in Equation [2] were exposed when the model was extrapolated beyond the scope of the modeling dataset. Validation of Equations [1] and [2] suggested that the models performed quite similarly on the validation dataset, with a mean residual that was only a third of a degree in vertical angle, an absolute deviation of approximately 8°, and a mean squared deviation that was very similar to the original model mean squared error (Table 5). A separate and truly independent database of branch angles, as would be available from CT scanning, would facilitate more rigorous validation (Table 5).

The model for HCB was required for backdating tree dimensions because, consistent with wide recognition of a functional link between stem profile and crown length (Larson 1963), the taper equations included live crown length as a predictor (Walters and Hann 1986). The HCB model (Equation [3]) explained 92.9% of the variation in height to crown base (Table 6), and behaved well by providing consistent declines in HCB as tree dimensions were back-predicted.

Models predicting knot pith curvature (Equations [4] and [5]) produced estimates consistent with a very limited number of observations of longitudinal-radial sections through knots (Figures 2

and 6). At the tree tip, the path of the knot pith is predicted to be nearly linear in the positive direction. As depth into crown increases, the knot pith becomes more curved towards a horizontal asymptote. Residuals for Equations [4] and [5] indicated homogeneity of variance and no apparent bias. Because Equation [1] smoothed away much of the variation in angles within and among branches, and was then used in constructing the modeling database, both Equations [4] and [5] explained nearly all of the variation in of the resulting knot pith curvature patterns (Table 7). Predicting H_{rib} from h_0 versus h_1 did not change the goodness of fit or residual behavior of Equation [4] or [5].

The simulated knots resembled curved cones, except that the rate of increase in knot diameter decreased with increasing distance from the bole pith (Figure 7). Knots near the tip of the tree (Figure 7 D) are oriented more vertically and increase in diameter rapidly throughout their length, whereas knots near the base of the crown (Figure 7 A) become more horizontal and are almost cylindrical in shape due to their slow growth rate deep in the crown.

Discussion

Mechanisms controlling branch angle and knot pith curvature

Models for knot pith curvature described in this paper predicted only the average trend for a branch within a given whorl. In reality, curvature of different knots would vary within a whorl, because they would exhibit the same degree of variability observed in branch angles within that whorl. Future analysis should consider how to translate the within whorl variation in branch angles into a corresponding set of stochastic knot pith curves. Sets of knot pith curves could be modeled by assuming a specific pattern of autocorrelation through a chronosequence, for

example, by assuming that branches remain in the same percentiles of the angle distributions at each whorl age. Alternatively, repeated measurements of specific branches could generate a time series that could be modeled directly, leading to a variety of knot curves within a given whorl. Regardless of the specific approach taken for developing them, a set of knot curves would allow stochastic simulation of knot shape in virtual logs and reproduction of the natural variability that would be observed in real logs. Knot attributes of products generated from simulated sawing of these logs would in turn be very realistic even though the mechanisms generating the variability may not be explicitly represented.

As more information accumulates, it is also conceivable that some of the mechanisms driving the variation in branch angle and knot curvature could be explicitly represented in the models. Branch angle variation within a whorl presumably results from responses to light gradients, light availability, and associated production and movement of growth regulators that influence the degree of apical control experienced by each branch (Blake et al. 1980; Wilson 1998, 2000). Manipulative experiments that test apical control seem to evoke different responses in different species. For example, removal of apical buds had relatively little effect on the growth of subordinate lateral branches in Nordmann fir (*Abies normanniana*) (Rasmussen et al. 2010). In a different type of experiment, the loss of apical dominance induced by second flushing in Douglas-fir was reversed by external auxin application (Cline et al. 2006). To our knowledge, no experiments have been conducted to test the effect of differential bud removals from branches within a whorl; however, it would be reasonable to infer that production and movement of growth regulators among branches would control variation in the tendency toward relative apical dominance and plagiotropy within a whorl. Selective pressure for these mechanisms is likely

imposed because they generate a crown architecture that optimizes light interception (and ultimately reproductive success).

Other sets of mechanisms influence average branch angle independently of tree height and diameter, and could therefore also help refine the accuracy and precision of knot curvature models. For example, it has been demonstrated that branch angle is partly controlled by genetics (St. Clair 1994). Most forest growth and yield experiments do not take into account the genotype or family of subject trees, unless the field trials are progeny tests designed specifically for tree breeding purposes (Howe et al. 2006), realized gain trials designed to test different mixes of families (e.g., St. Clair et al. 2004), or clonal tests to identify the best performing genotypes (Li et al. 2015). St. Clair (1994) found that individual tree heritability (h^2) of Douglas fir branch angle was only 0.06 in one progeny test in the Oregon Coast Range, with angles ranging from 32-78° among individual trees and from 51-59° for averages among different families. However, others have found heritability as high as 0.49 (Biro and Christophe 1983) and 0.73 (King et al. 1992). St. Clair's (1994) results suggest that within a site much of the variation in branch angle is environmentally controlled by the factors referred to above, (i.e., gradients in light intensity). Branch angle will also have influence on crown width (Roeh and Maguire 1997) and therefore may have implications for heritable aspects of crown architecture that influence productivity (Chmura et al. 2007). Although some genetic gain from branch angle selection may be possible if more horizontal or more vertical branches were deemed desirable from either a growth or wood quality perspective, the low to moderate heritability of branch angle and apparent strong influence of the light environment suggest that tree improvement efforts might be better focused on wood properties that have been shown to be more strongly heritable (Howe et al. 2006).

364
365 Additional variation might be explained by measuring promising environmental factors
366 associated with site-to-site variation (Hein et al. 2007), after controlling for genetic effects on
367 branch angle. The implication of these effects on wood properties, through their effects on
368 branch angle and corresponding impact on knot curvature and its variability, have not been
369 previously assessed despite the fact that wood properties are known to vary along environmental
370 gradients in Scots pine (Høibø and Vestøl 2010) and Norway spruce (Moberg 2006)

371
372 *Applications and limitations*

373 Predicting knot pith curvature from a predicted or measured time-series of branch angles and
374 reconstructed *dib* profiles is a non-destructive sampling approach that is applicable to monitoring
375 permanent plots, but becomes logistically more difficult and more expensive as trees become
376 taller. Furthermore, branch angles predicted by Equations [1] and [2] apply only to the average
377 of primary branches formed in annual whorls of Douglas-fir. Insertion angle of interwhorl and
378 epicormic branches can be measured and curvature of resulting knots can be estimated on these
379 types of branches in the same way as on whorl branches. Although these branches have been
380 shown to carry a significant amount of foliage in Douglas-fir and therefore may be important for
381 tree growth (Jensen and Long 1983), they have relatively little influence on the properties of
382 structural lumber. Results from both product recovery studies (Fahey et al. 1991) and lumber
383 testing (Whiteside et al. 1977) have indicated that the expected strength of Douglas-fir lumber is
384 correlated with the largest knots in logs and sawn products.

385

A key assumption in reconstructing knot pith curves from the chronosequence of branch angles was that the tree growth rate in diameter and height maintained the same proportion of the potential growth curves over time. This assumption would hold best for trees in even-aged stands with no silvicultural intervention. Increasingly complex silvicultural regimes will require that the data represent a true time series collected as repeated measurement of individual branches, or that CT scanning techniques be applied to destructively sampled trees near the end of a rotation. Crown responses to thinning and to fertilization (assuming a growth response) would include abrupt shifts in diameter growth and quite possibly in branch angle as well. An advantage of repeated measurements is that, from a silvicultural viewpoint, more insight into the biological causes of internal knot geometry would be gained by directly observing the external response of branches to silvicultural treatments of known intensity. Repeated measurements of branch angle also provide an attractive alternative to destructive sampling, intensive stem dissection, or CT scanning in species of low value or in other situations where resources are limited for modeling knot shape.

The approach applied in this analysis also can facilitate distinction of the live or tight knot zone from the dead or loose knot zone. Repeated application of the height to crown base model to determine the year of whorl branch mortality provides direct estimation of the live/dead knot transition.

The dataset used in this analysis came from relatively young, planted Douglas-fir trees (Table 2). To better understand the change in branch angles on planted Douglas-fir over time, additional data should be collected from larger trees, across additional explanatory variables, and over time

on individual branches. Because it is likely that average branch angle near the tip of the tree (at a given depth into crown) will change as trees age, grow in height, and experience lower water potentials near the top, it would be highly desirable to measure angle on some branches closer to the tree tip than can be accessed by climbing (Table 3). Measurements on these youngest branches should facilitate more dependable estimation of the lower asymptote to branch angle as depth into crown approaches zero (Equations [1] and [2]). More vertical branches increase the effective knot size in wood products sawn parallel to the bole pith. For example, a 3-cm knot through a board of any width would contribute a 30% higher knot volume if it was formed at an angle of 50° relative to perfectly horizontal (90°). On the other hand, branches with the lowest angle of insertion are also the youngest, so as mentioned above, their influence is most pronounced within the low-quality juvenile wood core rather than in high-quality mature wood. Micro-anatomical attributes such as cell wall thickness, latewood proportion, wood density and microfibril angle are more important determinants of wood quality and value in the juvenile wood core, relative to branch diameter and angle, minimizing the importance of branch measurements near the top of the tree where this wood is formed.

Conclusions

Our procedure for constructing a modeling dataset required only three analysis steps: (1) reconstruction of the stem *dib* profile for each year of past tree growth; (2) prediction of branch angle for each year of branch growth (Equation 1); and (3) numerical solution to find the *x-y* coordinates for the intersection of stem *dib* profile and the branch or knot pith in that year. Using this approach it was possible to model the arc formed by the knot pith at various heights on a Douglas-fir tree. With an assumption of knot size based on modeled trends in BD_{max} it was

possible to generate a three-dimensional knot. The next step in developing this approach should be validation of models describing knot geometry, preferably by X-ray tomography of whorl sections taken across a wide range of tree size and growing conditions, covering at least the range used for model development (Tables 2 and 3). The knot mapping software, “Gourmands”, described by Tong et al. (2013) and developed at the Institut National de la Recherche Agronomique (INRA), demonstrates the potential of X-ray tomography for validation.

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Tables

Table 1. Definitions and units of variables used in modeling Douglas-fir branch angle and knot pith curvature.

Variable	Definition	Units
VBA	Branch angle from vertical	°
CL	Crown length	m
HT	Total tree height	m
HCB	Height to the crown base	m
DBH	Diameter at breast height	cm
BR_{ht}	Branch height at insertion	m
HT_{rel}	Branch height at insertion relative to HT (1 at tree tip to 0 at tree base)	-
BD	Branch diameter at the point of insertion	mm
SI	Site index at a base of 50-years	m
$DINC$	Depth into crown	m
$DINCR$	Relative depth into crown (1 at HCB to 0 at HT)	-
H_{rib}	Increase in knot pith height from height where knot pith intersects tree bole pith	cm
rib	Radial distance from the tree bole pith	cm
rib_1	Radius inside bark of the tree at height of knot pith emergence from cambium	cm
rib_0	Radius inside bark of the tree at height of intersection of knot pith and tree bole pith	cm
h_1	Height of knot pith at emergence from the cambium	m
h_0	Height of knot pith at intersection of knot pith and tree bole pith	m

Table 2. Attributes of Douglas-fir plots and installations on which sample trees were measured for branch angle and diameter. Trees were sampled from 38 plots on 10 Stand Management Cooperative Type I installations and 16 plots on 6 Type II installations.

Attribute	Mean	Standard Deviation	Minimum	Maximum
Type I:				
Total basal area ($\text{m}^2 \text{ ha}^{-1}$)	10.4	7.6	0.8	26.1
Relative density (%)	18.8	12.8	2.1	45.1
Trees per hectare	703	447	188	2,085
Breast height age	9	3	3	14
Elevation (m)	368	224.5	167.6	822.9
Site index (m)	36.5	3.6	27.4	42.6
Type II:				
Total basal area ($\text{m}^2 \text{ ha}^{-1}$)	32.2	7.1	19.9	41.5
Relative density (%)	44.8	9.6	29.7	62.2
Trees per hectare	680	226	420	1,384
Breast height age	21	4	16	27
Elevation (m)	406.5	226.8	104.8	731.5
Site index (m)	36.5	3.3	32	41.1

Table 3. Attributes of Douglas-fir trees measured for branch angle and diameter. Angles of origin were measured on 15,662 branches from 287 trees on 10 Stand Management Cooperative Type I installations and from 2,291 branches from 125 trees on 6 Type II installations.

Attribute	Mean	Standard Deviation	Minimum	Maximum
Type I:				
DBH (cm)	14.5	5	3.3	26.6
HT (m)	10	3.1	3.8	22.5
CL (m)	9	3	2.7	20.9
VBA (°)	67.9	12.7	0	160
BD (mm)	20.9	6.9	1	75
HT _{rel}	0.3	0.1	0	0.8
Type II:				
DBH (cm)	28.3	6.7	14.8	46.2
HT (cm)	22.1	4.7	14.3	34.6
CL (m)	19.4	5.1	11.3	32.9
VBA (°)	74.6	10.9	3	138
BD (mm)	22.9	6.7	5	64
HT _{rel}	0.2	0.09	0	0.5

Table 4. Parameter estimates and fit statistics for the models describing the vertical trend in branch angle (Equation [1] and Equation [2]). All p -values of estimated parameters were less than 0.001.

Parameter	Variable	Estimated value	Standard Error
Equation [1]			
ω_0	-	37	-
ω_{11}	<i>CR</i>	10.7130	1.5767
ω_{12}	-	35.1457	1.5161
β_{11}	<i>DINCR</i>	-1.1599	0.0719
β_{12}	<i>CL</i>	-0.0623	0.0057
β_{13}	<i>DBH/HT</i>	0.3026	0.0363
		RMSE: 11.43	R ² : 17.6%
Equation [2]			
ω_0	-	37	-
ω_{21}	<i>CR</i>	8.3492	1.2202
ω_{22}	-	38.1013	1.0207
β_{21}	<i>DINCR</i>	-1.2481	0.0637
β_{22}	<i>CL</i>	-0.0265	0.0051
β_{23}	<i>DBH</i>	-0.0432	0.0039
β_{24}	<i>BD</i>	0.03755	0.0025
		RMSE: 11.16	R ² : 21.5%

Table 5. Mean fit and validation statistics for Equation [1] and Equation [2]. Validation data consisted of 3,281 branch angle measurements from 14 plots and 9 installations in the Roeh and Maguire (1997) dataset.

Equation	Dataset	Mean D	Mean AD ($^{\circ}$)	Mean D^2
Equation [1]	Modeling data	-0.03	8.59	130.61
	Validation data	-0.14	8.70	143.99
Equation [2]	Modeling data	-0.05	8.38	124.39
	Validation data	-0.32	8.23	130.58

Table 6. Parameter estimates for modeling height to crown base using Equation [3]. All p -values of estimated parameters were less than 0.001.

Parameter	Variable	Estimated value	Standard Error
α_0	-	2.5857	0.0138
α_1	HT	-0.0847	0.0002
α_2	HT/DBH	-1.7064	0.0085
α_3	SI	-0.0133	0.0003
		RMSE: 2.58	R^2 : 92.9%

Table 7. Parameter estimates for Equation [4] and Equation [5] describing knot pith curvature in Douglas-fir trees. All *p*-values of estimated parameters were less than 0.001.

Parameter	Variable	Estimated value	Standard Error
Equation [4]			
γ_{10}	-	1.4817	0.0072
γ_{11}	<i>CL</i>	-0.0043	0.0001
γ_{12}	<i>DBH/HT</i>	-0.1187	0.0035
γ_{13}	-	0.1501	0.0008
γ_{14}	<i>rib₀</i>	-0.0052	0.0000
γ_{15}	<i>h₀/HT</i>	-0.0867	0.0009
		RMSE: 0.18	R ² : 99%
Equation [5]			
γ_{20}	-	1.4803	0.0072
γ_{21}	<i>CL</i>	-0.0043	0.0001
γ_{22}	<i>DBH/HT</i>	-0.1182	0.0034
γ_{23}	-	0.1506	0.0008
γ_{24}	<i>rib₁</i>	-0.0052	0.0000
γ_{25}	<i>h₁/HT</i>	-0.0869	0.0009
		RMSE: 0.18	R ² : 99%

Figure captions

Figure 1. Longitudinal-radial section from a Douglas-fir stem exposing the bole and knot pith.

Figure 2. One segment of a tree with annual stem growth layers reconstructed using a *dib* taper model (Walters and Hann 1986) and a superimposed time-series of branch angles. Points identify the numerical solution for the intersection of ($dib/2$) and knot pith for each year. A photograph of a similarly sized tree section is provided for reference.

Figure 3. Residuals from Equation [1] for describing the trend in vertical branch angle plotted against predicted branch angle and relative depth into crown.

Figure 4. Observed branch angle (from vertical) over relative depth into crown by quantile of crown length (m) from the Roeh and Maguire (1997) dataset, with trend in branch angle for the median tree of each quantile predicted using Equation [1].

Figure 5. Vertical trend in branch angle predicted by Equation [1] and Equation [2] for three trees covering the size range of the Roeh and Maguire (1997) dataset.

Figure 6. Knot pith curvature predicted using Equation [5] for branches at several heights (h_l) on a large tree from the Roeh and Maguire (1997) dataset ($DBH = 46$, $HT = 31$, $CL = 29$). The left panel depicts knot curvature on a relative scale in the stem profile (i.e. height of knot pith divided by maximum height of knot pith; distance from bole pith divided by radius inside bark) and the right pane depicts knot curvature on an absolute scale.

Figure 7. Knot geometry for a typical tree in the Roeh and Maguire (1997) dataset ($DBH = 26$, $HT = 16$, $CL = 14$), predicted using Equation [5], Equation [6] and a branch diameter model (Weiskittel et al. 2007a) at several heights along the stem (h_l): (A) 4 m, (B) 10 m, (C) 12 m and (D) 14 m.

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Figure 6.

Figure 7.