

Review

Effects of Silviculture and Genetics on Branch/Knot Attributes of Coastal Pacific Northwest Douglas-Fir and Implications for Wood Quality—A Synthesis

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Abstract: Douglas-fir is the most commercially important timber species in the US Pacific Northwest due to its ecological prevalence and its superior wood attributes, especially strength and stiffness properties that make it highly prized for structural applications. Its economic significance has led to extensive establishment and management of plantations over the last few decades. Cultural treatments and genetic improvement designed to increase production of utilizable wood volume also impact tree morphology and wood properties. Many of these impacts are mediated by crown development, particularly the amount and distribution of foliage and size and geometry of branches. Natural selection for branch architecture that optimizes reproductive fitness may not necessarily be optimal for stem volume growth rate or for wood properties controlling the quality of manufactured solid wood products. Furthermore, Douglas-fir does not self-prune within the rotation

lengths currently practiced. This paper synthesizes extensive Douglas-fir research in the Pacific Northwest addressing: (1) the effects of silviculture and genetics on branch structure and associated consequences for wood quality and the product value chain; and (2) methods to measure, monitor, modify, and model branch attributes to assist managers in selecting appropriate silvicultural techniques to achieve wood quality objectives and improve the value of their Douglas-fir resource.

Keywords: Douglas-fir; wood quality; silviculture; branch; genetics

1. Introduction

The natural dynamics of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands lead successively through stages of crown closure, branch suppression, and branch mortality near the crown base, with gradual rise in the base of the live crown, slow sloughing of dead branches, and eventual production of clear, knot-free wood typified by the clear bole surfaces of relatively old trees. However, early researchers in the Pacific Northwest of North America (PNW) found that Douglas-fir branches commonly persist for 80 years or more before they self-prune through the process of suppression mortality, decay, and physical sloughing of the dead branches [1]. This age is well beyond current harvest age of 40–60 years, so branches and their manifestation as knots in logs and wood products are an important determinant of quality and value. Branches support the photosynthetic factory of the tree, so their structure has been naturally selected to ultimately optimize reproductive fitness, influencing various functions such as orientation of foliage for photosynthesis, resistance to wind and snow damage, and effective pollen production, dispersal, and reception. Timber growers have focused on silvicultural practices, including genetic improvements that maximize stemwood production. Branching attributes of managed stands respond to these manipulations, but branching habit and crown form are also influenced by a variety of inherent site factors that include soil, topography, and climate that are beyond the capability of managers to control.

When the stem is converted to logs and then solid wood products, the live and dead portions of branches within the stem become knots that lower product strength and stiffness, contribute to warp, and reduce aesthetic value (with certain exceptions such as knotty paneling). Consequently, knots are a major cause of lower product volume and value recovery from logs [2]. The value chain recognizes low product value by transferring it back to lower log value and lower value of standing timber for landowners. As a result, forest managers, silviculturists, and geneticists have extensively explored the potential for techniques that would minimize branch size and number and their effects on log value.

Our objective is to synthesize silvicultural, genetic, and wood quality research on branch attributes and knot formation in Douglas-fir, including methods to measure, monitor and simulate branch formation, growth, and mortality, and to draw conclusions about the potential for modifying branch size and distribution to enhance product value. We focus on Douglas-fir as the economically most important species in the PNW, but the concepts and approaches are applicable to characterizing primary branches and their implication for knot attributes, wood quality, and productive value in other softwood timber species as well.

2. Branch/Knot Geometry and Physiology

A key feature of the xylem from a wood quality perspective is the relative orientation of longitudinal tracheids. Tracheids formed by the cambium of the branch are parallel to the branch axis while the tracheids formed by the stem cambium are parallel to the main axis of the tree stem. Therefore, the angle of branch tracheids relative to the stem tracheids most commonly ranges from 60–90 degrees, although angles approaching 0 degrees (near vertical) are sometimes observed, as are sagging branches that exceed 90 degrees from vertical. Due to this change in angle, tracheids formed at the stem—branch junction give rise to the “distorted grain” surrounding knots in manufactured products, leading to points of lower strength and stiffness.

Most branches originate from lateral buds of new shoots and have cambial growth, phloem, and xylem that are integral with that of the stem. This provides for continuous translocation of water and nutrients to branches and foliage, and for transport of photosynthates from foliage to the stem and roots. As a result, cells in the branches are integrally connected with cells in the main stem while alive, but they are eventually overgrown by and embedded in stemwood after they die. As a particular branch and the stem continue to grow, the branch increases in diameter, increases in distance from the terminal shoot, and experiences shading from higher branches within the tree and from neighboring trees. Eventually, this shading reduces light below the intensity required to support the branch (light compensation point), resulting in death of the branch and recession of the live crown base up the stem. During this process, the branch cambium dies back to the bole surface and the diameter of the branch has reached its maximum. The stem begins to grow over the dead branch and eventually the encased branch or knot becomes smaller at the bole surface due to branch taper, drying and shrinkage, and eventual sloughing of the bark and decay of the branch wood. Because measuring branch size when grading trees and logs in an operational setting focuses on branch or knot diameter on the stem/log surface, it becomes important to understand the implications of this surface measurement for internal branch or knot size and shape. Branch diameter on trees and logs can be measured destructively or non-destructively, depending on the objectives of measurement and intended research or operational applications. A cross-section through the branch allows measurement of annual diameter increment. Branch diameter follows a sigmoid growth pattern over age, with time to reach maximum diameter dependent on growing space, stand dynamics, branch longevity, and a variable period of continued survival with no visible increment [3]. Some researchers have used related rates allometry to correlate branch diameter growth with stem diameter growth [4].

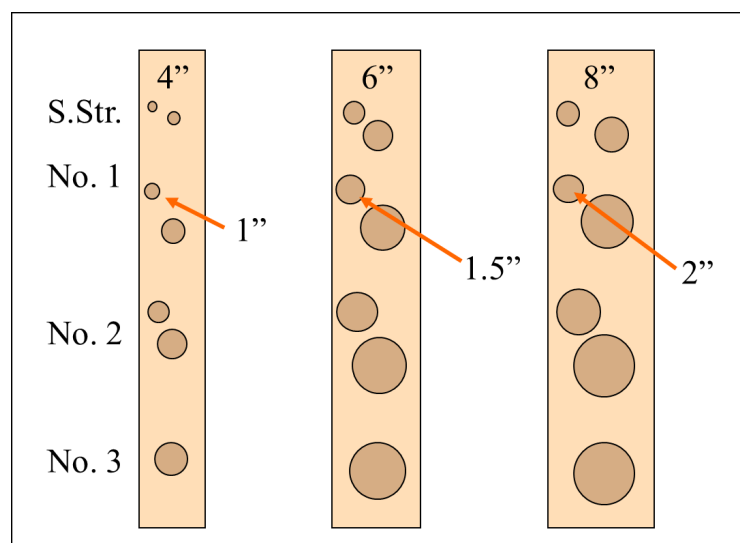
3. Branches, Knots and the Douglas-Fir Value Chain

Douglas-fir is one of the densest, and hence strongest and stiffest of softwood species. Its lumber is recognized for its mechanical properties and durability for structural applications. A wide variety of products are manufactured from Douglas-fir. These include appearance grade lumber where quality is based on the relative amount of clear wood (free of knots) and is influenced more by knot placement/pattern than size. Both knot pattern and size are important in traditional solid-sawn structural lumber and plywood and in engineered wood products such as glulam beams, laminated veneer lumber, I-beams, joists, and trusses that require a high level of stiffness [5].

While wood density plays an important role in the mechanical properties of lumber and engineered wood products, knots also strongly influence the grade and value of lumber, largely because of their effect on stiffness and strength. In lumber grading, knots are classified according to size, quality, and location. Allowable knot size is based on width of lumber and knot condition [6]. Knot quality, or condition, is described in many different ways. A knot formed from the live portion of the branch has its tracheids interconnected with those of the tree stem so is variously referred to as a live, intergrown, tight, sound, fixed, or red knot. A knot formed from the dead portion of a branch has tracheids that are structurally disjunct from the tracheids in the tree stem, so is referred to as dead, unsound, loose, or black. Along with this distinction between live and dead, knots are also described as star-checked (containing radial checks); firm (containing incipient decay); pith; or encased (not intergrown with surrounding wood) [7]. The synonym “loose knots” for dead knots underscores the fact that dead knots sometimes fall out leaving a hole. Knot location (e.g., edge) or occurrence (e.g., single) relates to the appearance of the knot on the lumber surface (e.g., spike knot) and hence results from log sawing pattern.

Different sets of grading rules are applied for different wood products in the PNW. Most lumber produced in the PNW is visually graded, and rules vary based on size and intended application. Structural light framing lumber is 2–4 in (5–10 cm) thick and 2–4 in (5–10 cm) wide, and structural joists and planks are 2–4 in (5–10 cm) thick and 5 in (12.5 cm) or wider [6]. Knots on the narrow surface of lumber are evaluated the same as knots on the edge of the wide face. The highest structural lumber grade allows sound, firm, encased and pith knots. The size of the knots allowed in a specific visual lumber grade is dependent on board width and location of the knot(s) within the piece (Figure 1). A study by Middleton and Munro [8] found that knots were the grade limiting defect in almost 30% of visually graded lumber.

Figure 1. Effect of lumber width and knot size and placement on visually graded dimension lumber.



Machine stress rated (MSR) lumber can be graded using MSR visual grades [6] and also non-destructively using such tools as a continuous lumber testing machine. Engineered products manufactured from lumber, such as glulam beams, laminated veneer lumber, or veneer used in plywood also rely on material of designated stiffness (Figure 2). Knot size and placement have an

effect on where failure under loading occurs, because grain distortion around knots represents a source of weakness (Figure 3).

Figure 2. Examples of engineered wood products, (a) glued laminated timber and (b) i-beams, that require high stiffness components; zones are indicated within each product where this property is specifically required.

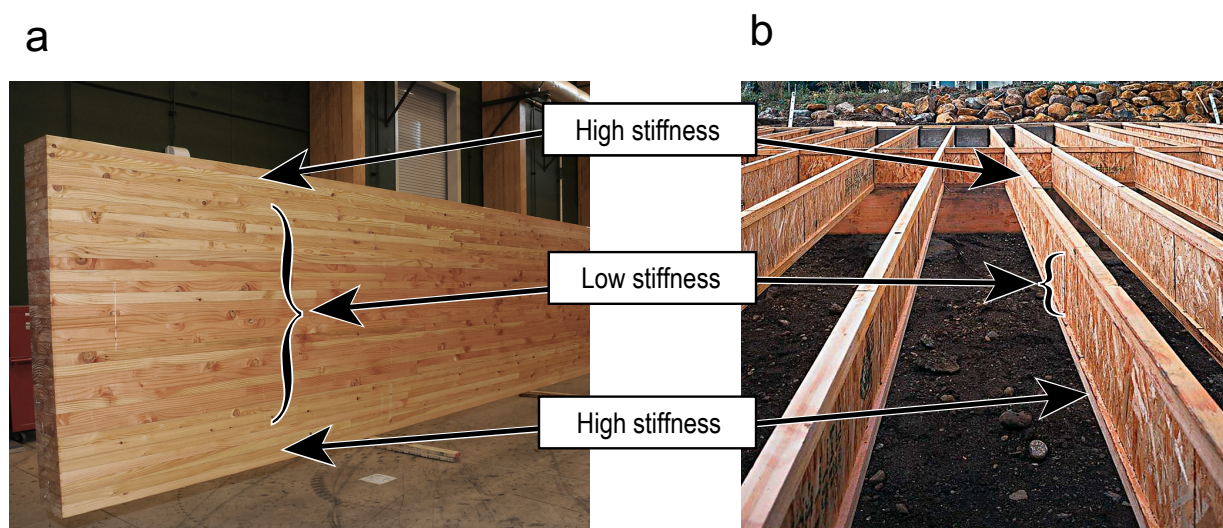


Figure 3. Failure under loading often occurs where edge knots or grain deviation around knots is present.



4. Important Log Characteristics and How They Can Be Assessed in Trees

Examination of log grades and sorts, product recovery studies, and discussions with log buyers indicate that the four following log characteristics predominate in log specifications: minimum rings per inch, minimum log diameter, maximum knot diameter, and maximum length [9–11]. Unfortunately, current log grades are not always indicative of lumber quality recovered during processing [2,12].

Log grades and sorts have knot diameter limits [13]. Product recovery researchers have found that a measurable log attribute referred to as largest limb average diameter (LLAD) [2], also known as branch index or BIX [9], is a good predictor of product grade recovery. LLAD is obtained by measuring the diameter of the largest knot in each lengthwise quadrant or face of the log and calculating the average (Figure 4). Visually graded lumber and veneer recovery is a continuous function of LLAD on Douglas-fir logs (Figure 5). Middleton and Munro [8] found average knot size to be a slightly better measure than LLAD but obtaining the average knot diameter is more time consuming. Regardless, the consistent result that product recovery is a continuous function of some

index of branch size underscores that log grades based on branch diameter thresholds are of questionable utility. One can hypothesize that, within a given tree, a measurement of knot diameter on the lower stem of a tree would be correlated with the LLAD of the first log, and perhaps upper logs, depending on the complexity of the stand density regime under which the stand was managed. One study in a 20-year old Douglas-fir spacing trial found that the diameter of the largest limb in the breast-height region (DLLBH) of trees is strongly correlated with both the LLAD and the largest branch diameter in the first 5-m log [14]. Where these correlations hold, they can be used to estimate LLAD from DLLBH, which is a simple tree measure that adds little to field time and cost. However, under intensive thinning regimes, maximum branch size increases in abrupt steps going up the stem, corresponding to the location of crown base when a thinning is implemented. After thinning, crown recession is temporarily arrested and branch longevity and size increase until the stand grows back to crown closure and crown recession recommences [15].

Figure 4. Method for calculating the largest limb average diameter (or branch index) for a log.

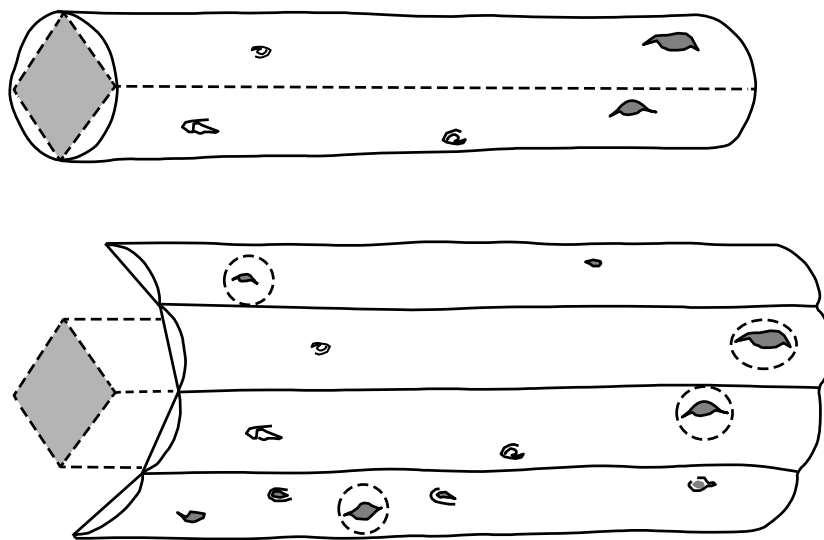
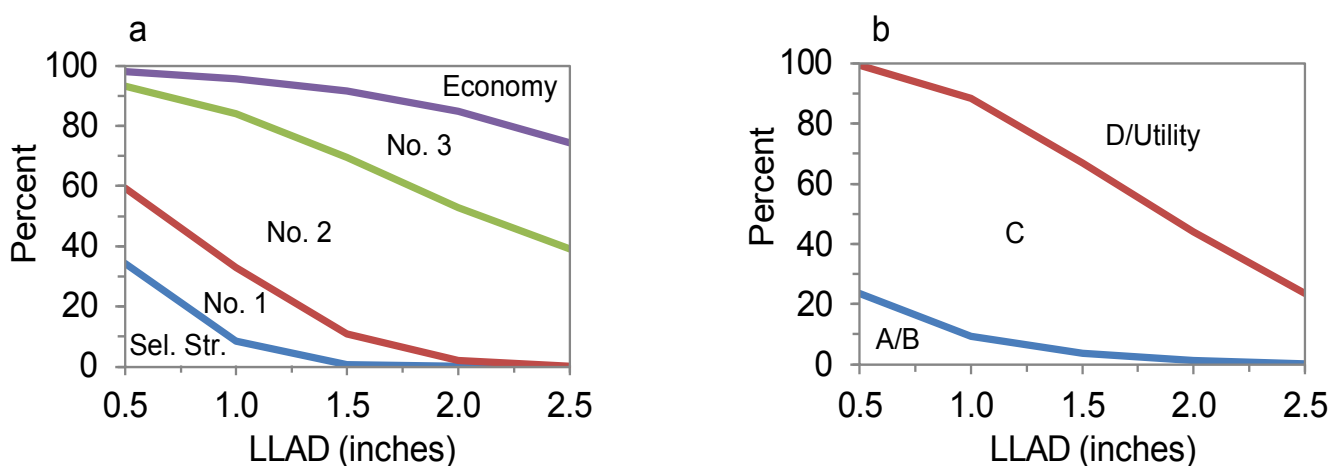


Figure 5. The effect of largest limb average diameter (LLAD) on the percent yield of visual grades of Douglas-fir (a) lumber and (b) veneer (from [2]).



5. Effects of Stand Density Regime, Fertilization, and Pruning

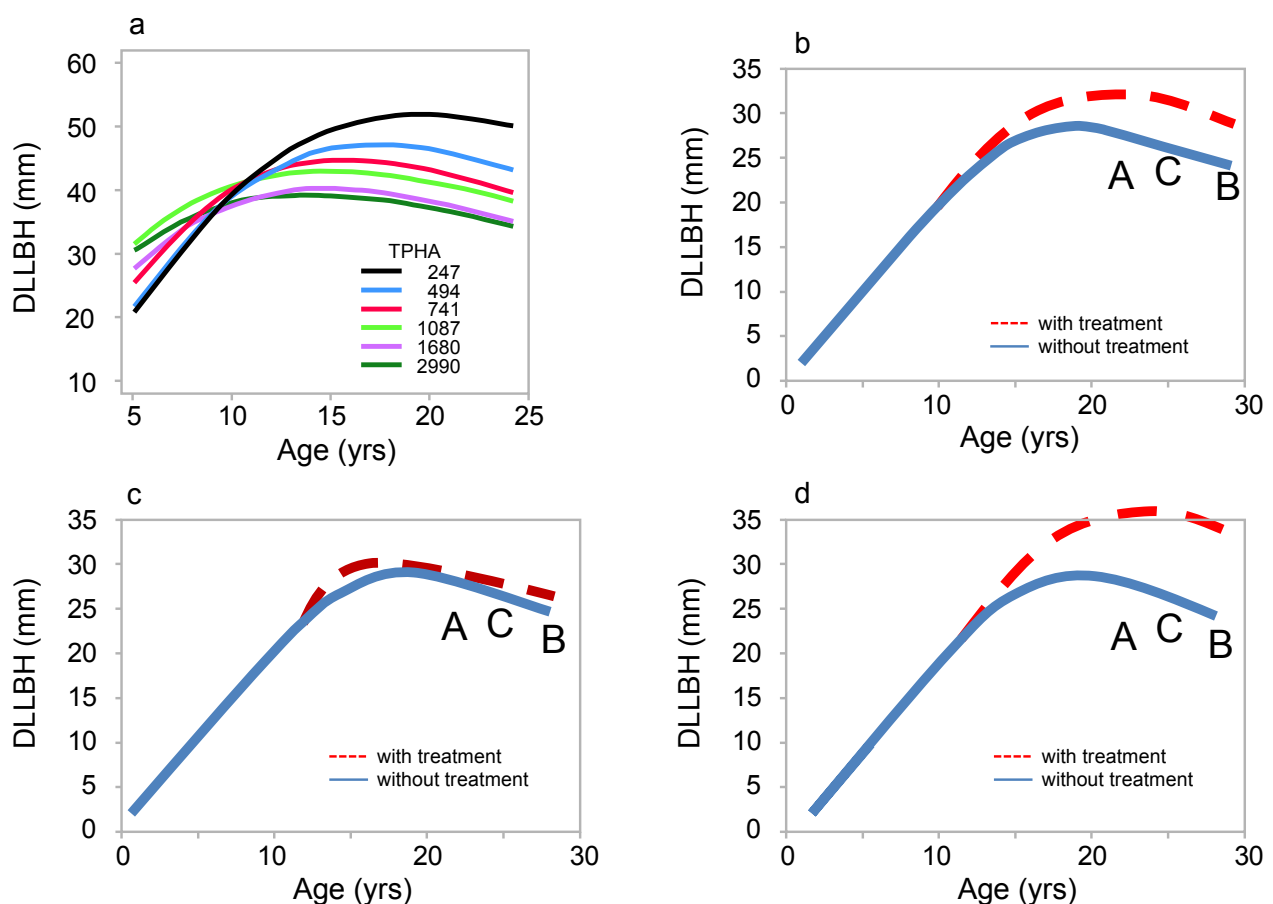
At stand establishment the base of the live crown is below breast height, so crown closure and crown recession begin earlier with closer initial spacing, with commensurate effects on branch sizes attained at time of suppression mortality [16]. Likewise, any subsequent thinning temporarily arrests or slows crown recession [17] and increases branch longevity and size [18]. The magnitude of this response to thinning depends on the intensity, type, and spatial distribution of the thinning. Fertilization is expected to produce additional branch diameter growth, but limited evidence to date suggests that the basic allometry between branch size and the combination of tree diameter, height, and crown length is not altered very dramatically (e.g., [19,20]), leaving little marginal effect of fertilization on maximum branch size at the tree level, beyond its direct effect on tree size. ANOVA of branch size on plots managed under various thinning and fertilization regimes by the Stand Management Cooperative (SMC) revealed significant differences in DLLBH between regimes [14,21–23]. DLLBH measured at the stem surface follows consistent patterns over time, as described above, but this general pattern varied among different silvicultural regimes, particularly if treatments are applied before branch mortality commences at breast height. Hypothesized trajectories of branch diameter at the bole surface over time and expected changes associated with initial planting density, thinning, fertilization, and thinning with fertilization are shown in Figure 6. DLLBH trajectories differ systematically over a range of initial planting densities [23]. During early stand development, trees planted at high densities develop larger branch diameter than those at low densities commensurate with tree size [24], but this eventually reverses (Figure 6a). Hypothetical effects of thinning and fertilization on DLLBH are shown in Figure 6b–d. The solid line represents a hypothesized trajectory of DLLBH over time and the dotted line represents the change that would occur in live branch diameter if the respective treatment were applied. The thinning effect (Figure 6b) on DLLBH is greater and longer term than that of fertilization (Figure 6c). However, combined thinning and fertilization (Figure 6d) have a greater impact than either treatment alone. Effect of treatment on dead branch diameter (at bole surface) is illustrated by points A, B, and C. If treatments were applied at point A, then branch diameter would decrease to point B due to increased dbh increment, but if untreated, would only decrease to C.

Regimes with relatively close initial spacing and no fertilization, with or without repeated subsequent thinning, have significant, but only slightly smaller, DLLBH than regimes involving fertilization [21,22]. Among plots receiving initial thinning at plantation age of approximately 10 years, no significant differences can be detected between DLLBH on trees grown under a given density regime and its fertilized counterpart; however, plots that had more moderate initial thinning and given multiple thinnings but no fertilization exhibit significantly smaller DLLBH than plots that are more intensely thinned and fertilized but not subsequently thinned [21].

Unlike thinning and fertilizing, pruning live branches immediately impacts branch and knot presence. Pruning a live branch abruptly halts the growth of live, red knots, and eliminates the formation of a dead, black knots provided the pruning is executed properly and the tree is capable of responding to the wound quickly by healing over the small branch stub. Following pruning, tree crowns are rebuilt by two key processes. First, because the upper crown branches remain in the same light environment after pruning as before, and also experience a likely increase in internal resources (water, nutrients), lateral elongation is increased compared to branches at the same height on unpruned trees [25]. Though it might be expected that branch diameter would increase concomitantly to support the longer branch, this was only beginning to be observed four years after pruning in stands that had

been intensely pruned (~60% of live crown removed). Second, under low stand density and >50% removal of live crown, the light environment in the lower portion of the pruned bole is significantly increased to the extent that epicormic branches may form from dormant buds [26]. These epicormic branches lead to pin-knots near the surface of the stem. However, these usually grow to only an inconsequential size by the time the remaining crowns rebuild and the canopy closes again. Pruning therefore leads to earlier clear wood production on a portion of the bole and does not appreciably impact branch growth and subsequent knot formation in the unpruned portion of the stem. However, the expense of operational pruning all branches in the lower bole has not proved economically viable for early clear wood production in the PNW.

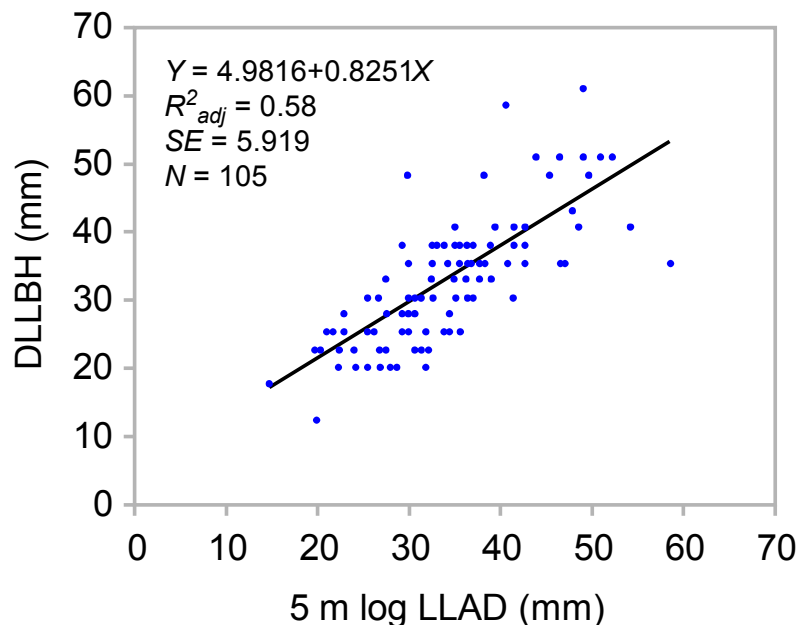
Figure 6. Hypothesized effects of (a) initial planting density (adapted from [23]) (b) thinning, (c) fertilization, and (d) thinning plus fertilization on branch diameter measured over time on the stem surface; in b-d dashed lines represent change in live branch diameter due to treatment; if treatment began when point A of a dead branch was at the stem surface, branch diameter would decrease to B; however, if no treatment occurred, branch diameter at the stem surface would only decrease to C due to slower dbh increment in absence of treatment.



Although these treatment regime effects on average attributes are important, timber and log purchasers are ultimately interested in the distribution of logs by specifications, in this case maximum branch diameter. The relationship between LLAD of the 5-m butt log and tree DLLBH (Figure 7) is highly significant, with DLLBH explaining 58% of the variation in LLAD [21]. This relationship can

translate a LLAD log specification into an equivalent DLLBH tree measure. For example, if a log purchaser specifies that LLAD cannot exceed 35 mm, mean DLLBH should not exceed 33.9 mm.

Figure 7. Relationship between largest limb average diameter (LLAD) of the 5-m butt log and diameter of the largest limb at breast height for the same tree (DLLBH) on plots from the Stand Management Cooperative Twin Peaks field trial (adapted from [21]).



6. Process Capability Analysis (PCA)

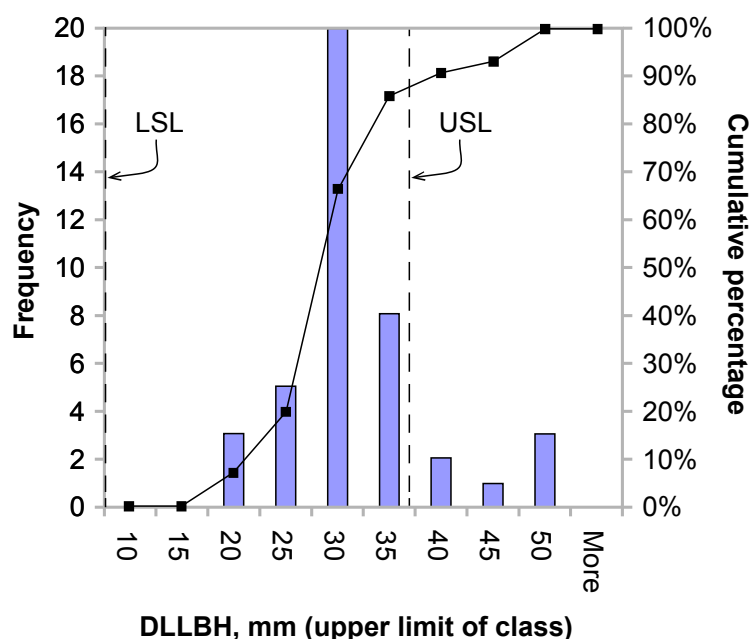
The preceding section demonstrates important effects of silviculture on branch/knot diameter observed on the surface of trees but how can timber buyers and sellers and forest managers compare these effects with market driven specifications? This can be accomplished using techniques from statistical quality control such as process capability analysis. Process capability is estimated by using a probability distribution with the shape, center (mean) and spread (standard deviation) appropriate for the product property of interest [27]. One context for process capability is “product characterization” usually expressed as the six-standard-deviation spread, known as “upper and lower natural tolerance limits” (UNTL, LNTL), of the property distribution. Since this definition only refers to the product property without reference to a specification or standard, a common second context of process capability is to express it as the percentage of product falling outside (not conforming), or within (conforming), to external “upper and lower specification limits (USL, LSL)” for the property. Specification limits originate from designers, engineers, product standards, or customers and may be one- or two-sided. The relationship between LLAD of the 5 m butt log and tree DLLBH (Figure 7) can be used as a one-sided specification limit. Here, a timber purchasing specification of $LLAD \leq 35$ mm translates into $DLLBH \leq 33.9$ mm, rounded to 34 mm, and used as a one-sided specification limit for the distribution of DLLBH of trees in a stand for the distribution of DLLBH of trees in a stand.

Process capability can be estimated by comparing the specification limits to either a theoretical probability distribution, if known, or to the actual frequency histogram of the property. Developing the frequency histogram of a property requires measuring the property on a sufficient sample. In

constructing frequency histograms, Montgomery [27] suggests using between 4 and 20 bins, “choosing the number of bins approximately equal to the square root of the sample size.” Thus to have 6 bins describing a property, the property should be measured on at least 36 product items.

A series of plots on an SMC research site initially planted with $1100 \text{ trees} \cdot \text{ha}^{-1}$ will be used as an example. Before the saplings reached crown closure some plots were left at the initial spacing (ISPA) and other plots were respaced to half this density (ISPA/2) and to one-quarter this density (ISPA/4). Some plots followed future thinning regimes based on Curtis’ relative density [28] and matching plots also received $224 \text{ kg} \cdot \text{ha}^{-1}$ nitrogen fertilization (F) as urea at the time of plot establishment and every 4 years thereafter until five applications were completed. A PCA was performed by superimposing regular and cumulative frequency distributions of DLLBH of 40 sample trees from each plot and the 35 mm USL. For the plot with repeated thinning and fertilization (ISPA_RT_F; Figure 8), 86% of the trees conform to the 35 mm DLLBH specification. Conformance for other plots varied from 100% in the plot with no thinning or fertilization (ISPA_NT_NF) to 64% in a widely respaced plot that was fertilized but not thinned (ISPA/4_NT_F) (Figure 9). In comparing unfertilized and fertilized plots (brackets), fertilized plots have conformance levels on the order of 10% to 15% lower than their unfertilized counterparts because respacing and initial fertilization occurred when the live crown was below BH. The timing of the treatments allowed branches at breast height to live longer and grow larger in diameter.

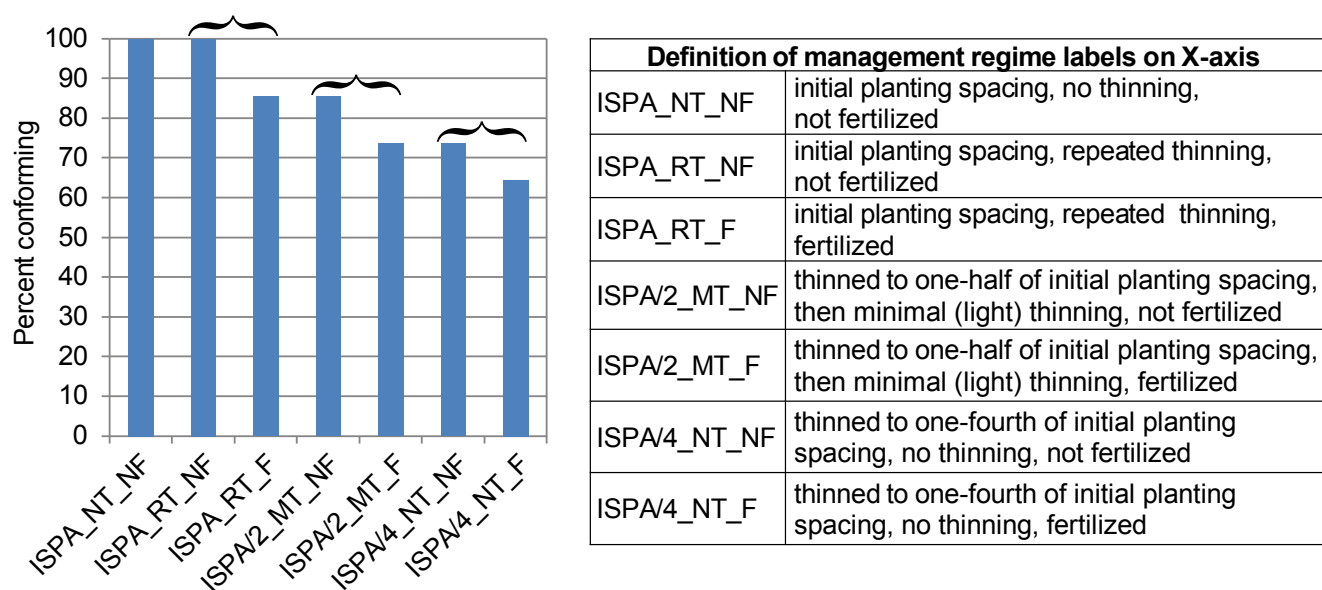
Figure 8. Frequency of DLLBH (diameter of largest limb at breast height) and conformance to a 35 mm upper specification limit for one plot at the Twin Peaks field trial (Initial Stems per Acre (ISPA) with Repeated Thinning (RT) and Fertilization (F); vertical dotted lines represent LSL (lower specification limits) and USL (upper specification limits) for DLLBH (adapted from [21]).



PCA is a simple, powerful method for integrating wood quality measurements during purchase or selling of timber, and for monitoring properties as stands develop over time [21]. It is a tool that can be

used to examine the conformance of various measurements from sample trees from different stands to determine the best stand for the mill to purchase. Information for PCA can also be simulated with growth models as shown in the next section, facilitating evaluation of wood quality ramifications of alternative silvicultural regimes.

Figure 9. Conformance of seven silvicultural regime plots on the Twin Peaks field trial to a 35 mm upper specification on DLLBH, the diameter of the largest breast height branch; bracketed pairs represent unfertilized vs. fertilized plots [21].



7. Modeling Branch and Crown Architecture

Branching structure and crown architecture have been modeled to address a very wide variety of objectives, from understanding the effects of primary branches on knot formation, to describing the three-dimensional framework for optimal foliage display and capture of solar radiation and understanding phylogenetic differences in plant form. Applications to wood quality have typically involved modeling the size and distribution of primary branches, *i.e.*, the branches attached to the main stem of the tree, because primary branches form the red (or live) knots while alive and black (or dead) knots after death (e.g., [29,30]). The ultimate objective behind the latter type of branch modeling work is to simulate the implications of alternative silvicultural regimes on log and wood product quality (e.g., [15,31,32]). The size attribute that has received the most attention is the largest or average branch diameter within a given whorl of branches, in part because as noted above the largest or average branch diameter within a log is a strong predictor of product recovery. Various model forms have been used, but because the trend in branch diameter through the crown [30] or through the full length of the tree [29] is nonlinear, the model form typically accommodates prediction of branch diameter as a function of depth into crown as well as basic tree dimensions that include DBH, total height, and crown length or crown ratio.

After estimating the largest branch within a whorl, the second most commonly modeled attribute is the number of branches at a whorl or within an annual segment of the main stem [20,30,33]. Both whorl and interwhorl branches are formed in Douglas-fir, but unlike true firs (genus *Abies*), the distinction

between whorl and interwhorl branches becomes rather arbitrary. The interwhorl branches are probably inconsequential from a knot size and wood quality perspective, and pines (*Pinus* spp.) do not form interwhorl branches, so the emphasis has often been placed on the number of whorl branches only.

Branch angle can also be an important attribute because this angle controls the degree of grain distortion in the vicinity of a live knot. In Douglas-fir and other species, branch angle generally increases with depth into crown [30,33,34]. Because this pattern implies that the angle of a given branch increases over time, a longitudinal cross-section through the main stem and branch axis shows the arc defined by the branch pith going from the center to the surface of the stem. The geometry of the branch internal to the tree has been modeled to facilitate simulated sawing and peeling of logs and implied location and shape of three-dimensional knots within manufactured products [35].

From the perspective of inventory, the practicality of measuring branch diameters on standing trees can be challenging; therefore, as mentioned above some work has been done on analyzing the performance of maximum branch size in the first whorl above breast height (DLLBH) for estimating the largest limb average diameter (LLAD) [14]. This conversion allows application of LLAD in Douglas-fir product recovery equations [2]. Because DLLBH changes over time as described above, models have been developed to track the change in DLLBH over time [23].

Two basic approaches have been taken for linking growth model output containing log quality parameters to product and value recovery, *i.e.*, product recovery equations and simulated milling. Product recovery of Douglas-fir lumber and veneer from individual logs was measured in a large mill study of logs from Oregon and Washington, yielding equations that predict visual and MSR grades as a function of LLAD and proportion of juvenile wood (Figure 5), the latter defined as wood formed within 20 years of the pith [2]. A wood quality output file is available from the growth model ORGANON [15], and has been used in combination with these product recovery equations to assess the economic performance of alternative silvicultural regimes [31]. Although application of the product recovery equations [2] requires adherence to a 20-year definition of juvenile wood core, ORGANON allows the user alternatively to define juvenile wood as crown wood, in recognition of the fact that more extreme stand densities result in departures from the 20-year average resulting from historically implemented stand density regimes. The output from ORGANON can be used to assess effect of silvicultural regime on branch size in numerous ways, for example, distribution of butt logs by maximum branch diameter class (Figure 10), or vertical trends within trees that show the effects of initial spacing (Figure 11) or repeated thinning [15]. Although some companies in the U.S have proprietary sawing simulators, none are publicly available for Douglas-fir in the Pacific Northwest. Mitchell [36] developed a sawing simulator as part of SYLVER, a system for linking growth predictions from the growth model TASS [37] to product recovery and valuation. A sawing simulator developed for radiata pine (*Pinus radiata*) in New Zealand, AUTOSAW [38], has been adapted to Douglas-fir, but grade recovery could not be accurately determined for Douglas-fir based on surface knot characteristics [19,39]. No PNW Douglas-fir growth model is specifically linked to this sawing simulator, so economic analyses based on product recovery from sawing simulation are possible, but considerable post-processing of model output is necessary to provide input to the sawing simulator.

Figure 10. Results from ORGANON growth model simulations showing cumulative frequency of bottom 5-m logs by average maximum whorl branch diameter for six different

initial spacings (1.8, 2.4, 3.0, 3.7, 4.6, and 6.4 m) grown out to total age of 49 years; arrows indicate cumulative percentage of logs with average maximum whorl branch diameter less than 2.5 cm; under a 6.4-m spacing, 94% of the bottom 5-m logs have an average maximum whorl branch diameter exceeding 2.5 cm and 68% exceed 3 cm.

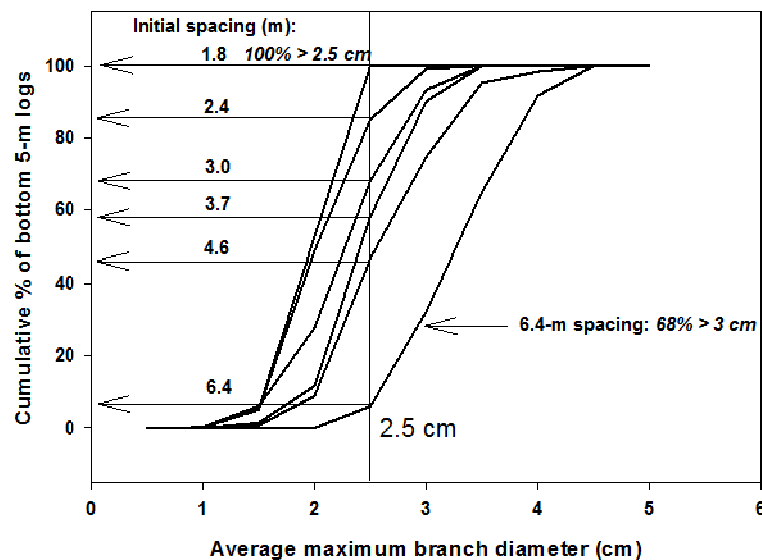
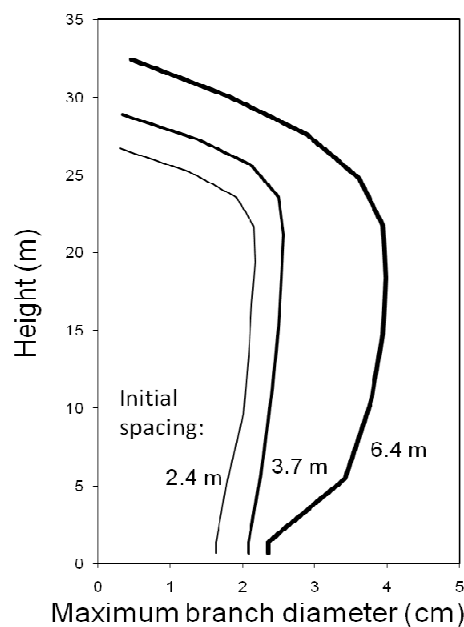


Figure 11. Results from ORGANON growth model simulations showing vertical pattern in maximum whorl branch diameter on the tree representing the 50th percentile of the dbh distribution under three different initial spacings (2.4, 3.7, and 6.4 m) grown out to a total age of 49 years.



8. Branch Traits and Douglas-Fir Tree Improvement Programs

Intensive tree improvement programs have been in place in the Pacific Northwest, both in the USA and Canada, since the 1950s. These programs are described by several authors (e.g., [40–42]). While the main emphasis has been on vigor, health and adaptability, the inheritance of several branch traits have been researched and two have been routinely scored in tree improvement programs. This work is described below.

8.1. Branch Number, Angle and Size

Large variation is clearly visible in branch number in young Douglas-fir in progeny tests and, to a lesser extent, in branch angle. Differences in branch size, on the other hand, are not readily apparent in progeny tests where trees are grown at uniform spacing. Visual log and lumber grading rules in the PNW penalize boards for large knots, but not for a large number of small knots (e.g., [6,43]). It has also been demonstrated repeatedly that knot size can be well controlled by density of planting and timing and frequency of thinning (e.g., [14]), and selection for clear wood stiffness was found more promising than selecting for smaller branch size when MOE of sawn lumber was assessed [44]. In contrast, stand density regimes (unlike genetic improvement) have little potential for manipulating frequency of ramicorn branches and forks. Likewise, genetic improvement programs cannot make simultaneous gains for a large number of traits and are already tasked with improving height, diameter growth and resistance to pathogens and insects, and reducing or managing incidence of forks, ramicorn branches and stem sinuosity.

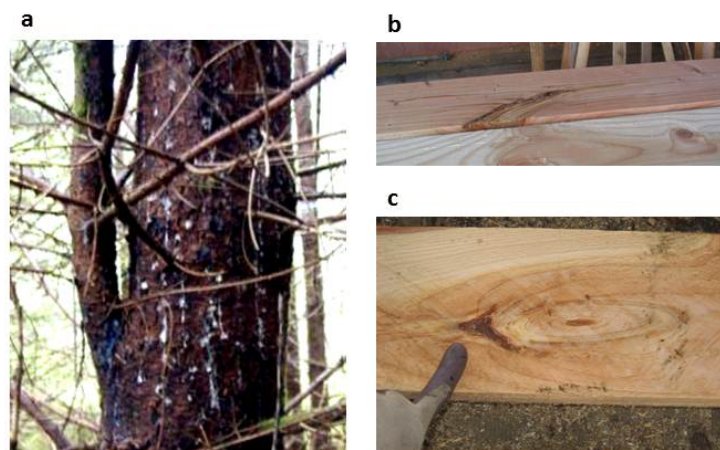
For these reasons there has so far been little serious effort towards improving these latter three traits, even though all have been shown to be heritable [45,46], and despite the variation observed. These branch traits were not recorded in first-generation or second cycle operational cooperative programs, so they had little impact on what trees were selected (apart from culling some individual forward selections with noticeably undesirable branching patterns). However, it is possible that selection for stem volume is causing a correlated increase in branch number and a decrease in branch size [45].

8.2. Ramicorn Branching and Stem Forking

Second flushing (lammas growth) in Douglas-fir often causes the leader to lose apical control. Under this condition, where the terminal bud breaks and the leader resumes growth in late summer, a second bud and a tuft of branches are formed at the end of the prolonged growing season. One of the lateral shoots (branches) will sometimes become the new leader, and the old leader becomes a steeply angled or ramicorn branch (Figure 12a). The alternate scenario is the lateral shoot becoming the ramicorn. Forks will also commonly develop after death or breakage of the top of the tree, causing two or more branches to turn up as a set of new leaders. Distinguishing ramicorn branches and forks is often difficult at the start, forks often downgrade to a ramicorn branch over time, and about a third of the trees with a ramicorn at age 12 had no ramicorn by age 24 [47]. Both these defects can lead to large economic losses to timber growers during bucking or log scaling; through (1) length deductions; (2) reducing a stem segment from a valuable long log to a lower value short log; or (3) reducing a stem segment from a valuable large diameter, single long log to lower value group of small-diameter, short

logs. These losses reflect the severe implications of ramicorn branches for solid wood products that contain associated defects (Figure 12b,c). Interest in these stem defects by tree breeders and forest geneticists goes back several decades (e.g., [48]).

Figure 12. Ramicorn branch on Douglas-fir tree (a) and implications for solid wood products manufactured from stem with ramicorn branch (b,c).



Forks and ramicorns have been routinely scored in cooperative tree improvement programs starting around 1990, as the frequency of trees with any of these traits (not the number of forks and ramicorns per tree). Currently forks are defined in cooperative programs as additional leaders exceeding 80% of the height of the tallest leader, while ramicorn branches are less than 80% of the height of the tallest leader. Ramicorn branching and stem forking are genetically controlled at the family level and the two traits are genetically correlated (Table 1; [49]). Genetic control is weak at the individual-tree level (weaker for forking than for ramicorn branching). The positive correlation at the family level (similarity of ranking for both defects) could be caused by several factors. Distinguishing between ramicorn branching and forks can be difficult, especially in thick foliage, and is complicated by the presence of other steep-angled branches. Second flushing can result in either a fork or a ramicorn branch being formed (*i.e.*, the same factor giving rise to both defects). Finally, the rapid growth associated with ramicorn branching may also leave leaders more susceptible to damage caused by birds, insects and snow break (potentially leading to forking). Genetic gains are possible, but typically the main emphasis has been to avoid losses compared to the native Douglas-fir population. There is unfortunately an adverse genetic correlation with growth rate, so the fastest growing families have a tendency to exhibit more ramicorns and forks than slow growing families [47,49].

Site productivity has a very strong influence on whether genetic propensity for ramicorn branching is expressed. For example, in one first-generation program with the same families tested on 10 sites, an R^2 of 0.97 was estimated between mean number of ramicorns/forks per tree, and the mean stem volume of that plantation (Northwest Tree Improvement Cooperative (NWTIC), unpublished data). As a result, most emphasis is placed on these traits where growth rate is expected to be particularly rapid, such as low-elevation sites with good soil and ample moisture. In addition to site effects, ramicorns and forks appear to increase under high-yield forestry (intensive site preparation, large seedlings, intensive weed control) unless we select genetically against them, and even intensive genetic selection is unlikely to reverse all the effects from site and cultivation treatments. Shorter rotations can also

increase the impact of these two defects, since small, young trees will have a larger proportion of the stem surface occupied by branches than large, old trees if all other factors (site, spacing) are kept constant [50].

Table 1. Across-site heritabilities and genetic correlation for incidences of forking and ramicorn branching, obtained at age-7 from second cycle tests in Douglas-fir in the Pacific Northwest of the United States; estimates for forking and ramicorn branching based on 70 sites and 174,738 trees, and 73 sites and 187,239 trees respectively (unpublished Northwest Tree Improvement Cooperative data).

Trait	Individual-tree Heritability		Family-mean Heritability		Genetic Correlation
	Narrow-sense	Broad-sense	Narrow-sense	Broad-sense	
Forking	0.02	0.02	0.34	0.40	-
Ramicorn branching	0.04	0.05	0.59	0.64	-
Forking:Ramicorn branching	-	-	-	-	0.52

The special case of pruning only the forks and ramicorns in the lower stem merits consideration due to the large economic impact of these two stem defects. Only the subset of final crop trees exhibiting those defects, and only a small number of branches for each of those trees, would need to be pruned (a much smaller effort than pruning all branches to produce clear lumber). This option needs to be compared with strong genetic selection against forks and ramicorns, or with deliberately avoiding some steps that maximize growth rate, because both of these latter approaches would come at a considerable loss in volume growth.

9. Conclusions

Douglas-fir is the most important commercial timber species in the U.S. Pacific Northwest. Arguably, knots are the greatest determinant of wood quality, especially given that current Douglas-fir harvest ages typically average approximately half the age when dead branches decay or slough off to allow the formation of clear wood. Knots strongly influence value in its two major product markets: (1) strength and stiffness of structural products; and (2) size and yield of millwork cuttings. Consequently, the presence of knots is a major criterion for assigning log and product grades.

Although branch characteristic of trees and the resulting knots in wood products could be controlled to some extent through genetics, tree improvement has been limited to minimizing stem forking and ramicorn branching. Branch diameter is much more strongly affected by stand density regime (initial planting spacing and the timing, intensity, and frequency of thinning), but less so by fertilization. Pruning to produce clear wood is not economically viable in current markets.

Statistical quality control has been adapted to measuring and monitoring branch diameter as stands develop and to final assessment of timber stands during marketing. These techniques are easily incorporated in growth and yield models, allowing managers to predict the effect of alternative silvicultural treatments on branch characteristics at time of harvest. These tools enable silviculturists to become more proactive in managing stand and tree quality as affected by branches and consequent knots in products.

Production of logs with given knot size indices can benefit from periodic sampling to monitor properties and joint conformance to a set of target specifications. Monitoring trees would also permit quantification and improved understanding of how treatment of a stand affects conformance. The concept of monitoring a process over time is embodied in the control chart approach of statistical quality control (SQC) [27]. Adoption of SQC for assessing and planning silvicultural actions should be investigated further.

Quantifying various timber characteristics based on customer specifications and stratifying a stand according to joint conformance provides a flexible method for presenting information to customers. Furthermore, it provides sellers with improved insight as to which customers are most likely to be interested in a stand so its marketing can be more targeted. Joint conformance information on the suite of stands scheduled for harvesting can be used to develop customized tree or log sort tables that can be integrated into decision support systems and models such as harvest scheduling and allocation. The integration of these one-time PCAs of marketable stands with harvest planning and allocation would add value to both seller and purchaser. The former benefits by having better information for targeted marketing while the latter has more assurance of purchasing stands that are well suited to its needs. Conformance information can also feed back to the design of silvicultural regimes and selection of genetic material for planting. By matching tree and stand characteristics to end product needs, appropriate allocation of resources along the value chain can be achieved.

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Author Contributions

All authors contributed towards the writing of the paper. Each had responsibility for at least one section and integrating their contribution with the overall paper.

Conflicts of Interest

The authors declare no conflict of interest.

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