S. Hummel, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, P.O. Box 3890, Portland, Oregon 97208

# Branch and Crown Dimensions of Douglas-Fir Trees Harvested from Old-Growth Forests in Washington, Oregon, and California During the 1960s


## Abstract

In temperate rainforests of western North America, some second-growth forests are managed to promote development of the multi-dimensional structures observed in old-growth forests. Information about tree architecture from across a range of growing conditions is needed to support this goal. Accordingly, branch and crown dimensions associated with tree age, site index, and stand basal area are reported for 854 Douglas-fir trees, which were harvested from old-growth forests in Washington, Oregon, and northern Califomia in the 1960s. Sample trees ranged from 38-647 years old. The average diameter and the relative height of the first live and dead branch increased with tree age. In contrast, only weak relations existed between live crown ratio, which was highly variable, and tree age or site index. Differences between old Douglas-fir trees and younger trees with an equivalent breast-height diameter (dbh) were greatest in the dimensions of their first branches. Between ages 100 to 500 yr, for example, the mean first live branch on a 127cm dbh tree was estimated to more than double in diameter-from 3.1 to 6.6 cm-at a basal area of 114 $m^2$/ha. Despite the limitations associated with inherited data, study results have silvicultural implications for managed Douglas-fir forests because they indicate that crown morphologies of large, young trees were not the same as their similarly sized, older counterparts on sites spanning a range of average natural stand density conditions within the Douglas-fir region.


## Introduction

When trees live for centuries and grow to be massive, measuring their branches and crowns is not easy. Nevertheless, such measurements can aid in understanding forest structural development and in designing and evaluating forest management practices. A need for information on the crown morphology of old trees exists in the temperate rainforests of western North America, where silvicultural treatments to create structural complexity in young forests are being applied with the objective of developing habitat for organisms associated with old forests (e.g., Beese and Bryant 1999, Carey et al. 1999, Franklin et al. 2002, Andrews et al. 2005). For example, the marbled murrelet *(Brachyramphus marmoratus)*, is one species whose life history includes big Douglas-fir trees *(Pseudotsuga menziesii)*, with large branches (Hamer and Nelson 1995). Managing forests to sustain such species requires information both about them and about the crown morphology of Douglas-fir associated with tree age and growing conditions.

In Douglas-fir/western hemlock forests *(Pseudotsuga menziesii* (Mirbel) Franco/ *Tsuga heterophylla* (Raf.) Sarg.) of the Pacific Coast ("Douglas-fir region"), evidence that age-related changes occur in the branches and crowns of Douglas-fir trees exists from a handful of studies on foliage distribution (Massman 1982), epiphyte communities (Pike et al. 1977), and crown shape (Ishii and Wilson 2001). Additional information on the branches and crowns of Douglas- fir trees, over a wider range of tree ages and growing conditions, would increase understanding about how the architecture (three-dimensional structure) of a large, young tree differs from that of a similarly sized, old tree.

To gain knowledge about the three-dimensional structure of old-growth Douglas-fir forests various techniques are used to access the canopy and measure the branches and crowns of tall trees, including climbing a tree or its neighbor (e.g., Ishii et al. 2000) and erecting nearby structures (e.g., Stork et al. 1997). New techniques for studying massive trees are being developed because destructive sampling, such as described in Gholz et al. (1979) or Monserud and Marshall (1999), is becoming less tenable as the population of old-growth trees declines. But non-destructive techniques can be time-consuming and expensive, which in turn can limit sample size. For example, some studies have investigated age-related changes in branch or crown dimensions of Douglas-fir by measuring a

[1] Email address:shummel@fs.fed.us

few young (20 and 40 yr) and old (450 yr) trees on one site in the region and then making inferences for the centuries in-between (Ishii and McDowell 2002, Moore et al. 2004).

This study adds to earlier ones by investigating how the branches and crowns of Douglas-fir trees change with tree age; it expands on them by investigating relations between branch and crown dimensions and stand basal area. To do so, I used measurements made on Douglas-fir trees harvested from old-growth forests in Washington, Oregon, and California in the 1960s. The data were collected by staff in the Douglas-fir Section of the National Log Grade Project (DLGP), a USDA Forest Service initiative to evaluate the quality of wood in standing trees for lumber and veneer production (Lane 1962). Early DLGP studies included tree, crown, and knot measurements because they are important considerations in assessing wood quality. The location and size of the first live and dead branch on each tree were also recorded because branch characteristics are the single most important factor influencing log grades (e.g., Makinen and Colin 1999). The branch data were not fully analyzed when they were collected, because the DLGP project focused on wood utilization rather than on tree architecture (e.g., Clarke 1960, Lane et al. 1973). They can now offer insight into the relations between tree age and crown dimensions of Douglas-fir trees. They restrict the analysis, however, to a chronosequence, which involves measuring trees of differing ages at a point in time rather than making repeated measurements on the same trees over time (e.g., Ishii and McDowell [2002]). The results expand on existing studies by investigating if branch and crown dimensions of young Douglas-fir trees differed from those of older trees having the same diameter.

## Methods

### DLGP Methods of Data Collection

Methods used to locate sample areas, select sample trees, and measure tree, branch, and crown dimensions were gleaned from published DLGP reports, notes left in project files, and interviews with retired Forest Service employees. The data reported in this paper were collected during DLGP lumber studies done between 1964 and 1967. Sample areas covered a range of site index, stand density, elevation, aspect, and soil type in Washington, Oregon, and California (Lane er al. 1973). For the DLGP a, "distinction between old growth and young growth was arbitrarily set at 100 years" (Lane et al. 1973: p. 1). Together with prevailing forest inventory methods (USDA 1957), this breakpoint age guided selection of sample areas by the DLGP. Sample areas were located on both private and public land in forest stands that were scheduled for imminent harvest.. Tree diameters were measured at 1.3 m above the ground. Stand age and tree ages were determined from ring counts on stumps (Lane et al. 1973), whereas stand basal area estimates were made with a prism. Individual stand growth history was not recorded.

Individual trees were selected based on size and stem quality. The DLGP goal was to obtain a representative sample of Douglas-fir commercial sawtimber (Lane et al. 1973) across a range of tree diameters and form classes. The prevailing form class used at the time was Girard, which is the percentage ratio of diameter inside bark at the top of the first standard log to diameter at breast height (dbh) outside bark (Husch et al. 2003). Form class is, therefore, an indicator of stem taper. Included in the DLGP sample were trees with observable defects, because a project objective was assessing how knot size, disease, or poor stem form reduced wood product recovery value. Excluded from the sample were trees with stems too defective to be sawn (Lane et al. 1973).

Measurements of sample trees (total height, dbh), their crowns (height to crown base), and branches (height to first live branch and first dead branch) were made before felling. Tools used at the time included Abney levels (Calkins and Yule 1935) for height and measuring tapes for diameter and length. Branch diameters (recorded in 1.27 em classes) and form classes were measured after felling with tapes or calipers at the stem (Figure 1).

### Selecting and Summarizing Historical DLGP Data

All records from the DLGP studies were first checked for obvious errors or omissions. Only studies with data for tree, crown, branch, and stand variables were selected. While null values were accepted, blank ones were not. These criteria resulted in selection of nine useable studies, three

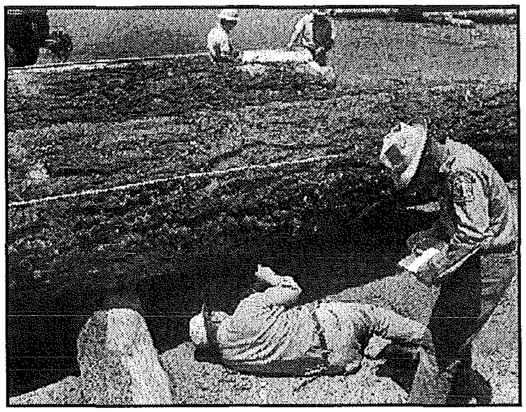

Figure 1. Forest Service crew measuring sample Douglas-fir tree for the Douglas-fir section of the National Log Grade Project (DLGP) (California 1965).

each from areas in northern California, Oregon, and Washington (Figure 2).

Within the nine studies, only sample areas with Douglas-fir trees classified in excess of 53.3 cm (21 in) dbh and usually over 180 yrs old were selected (following USDA 1957). According to DLGP protocols, for a tree species to be listed at a site it had to comprise at least 20% of the unit (by volume or basal area). Douglas-fir was listed first in all the records used for this analysis. Other species, in decreasing order of occurrence, were western hemlock, white fir *(Abies concolor* (Gord. & Glend.) Lindl., ex Hildebr.), sugar pine *(Pinus lambertiana* Dougl.), ponderosa pine *(Pinus ponderosa* P. & C. Lawson), mountain hemlock *(Tsuga mertensiana* (Bong.) Carr.), and redwood *(Sequoia sempervirens* (Lamb. ex D. Don) Endl.); their exact proportion in any sample area is unknown. Data for ten sample trees were discarded because of evident recording error. A total of 854 Douglas-fir sample trees in the nine historical DLGP studies contained complete records for all variables of interest. Consistency in measurement techniques was assumed because the same research team collected the data within a span of four years.

The raw tree data were used to calculate live crown ratio (LCR), the ratio of tree height to dbh (H/D), and the relative branch position for the first live and dead branch on each sample tree (after Husch et al. 2003). The LCR is the ratio of live crown length to total tree height, computed by subtracting the height to crown base (m) from the total tree height (m), with the result (crown

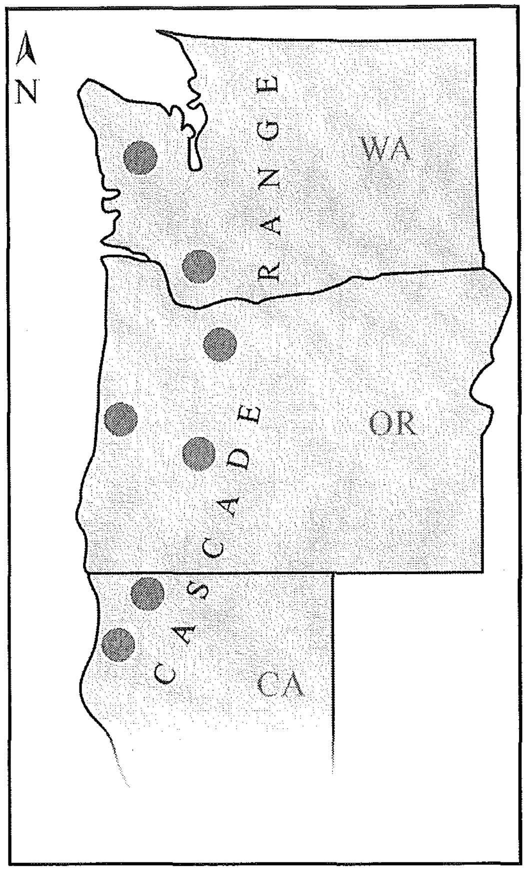


Figure 2. Sample areas for the location of the Douglas-fir section of the National Log Grade Project (DLGP) studies used in this analysis.

depth) divided by tree height. The H/D ratio is total height (m) divided by the dbh (cm). The relative position of the first dead branch and the first live branch is the branch height measurement (m) divided by total tree height (m). To organize analysis and reporting, I adopted three architectural categories-tree, crown, and branch. Basal area and site index were used as proxies for stand density and stand productivity, respectively, and are referred to collectively as stand attributes. Limitations on using basal area as a density measure are discussed in Davis and Johnson (1987).

The summary data were first examined to determine the suitability of grouping them by sample area. A covariance analysis was precluded because the range of tree ages represented in the full data set was not present in each area. For example, trees over age 500 were measured in only two

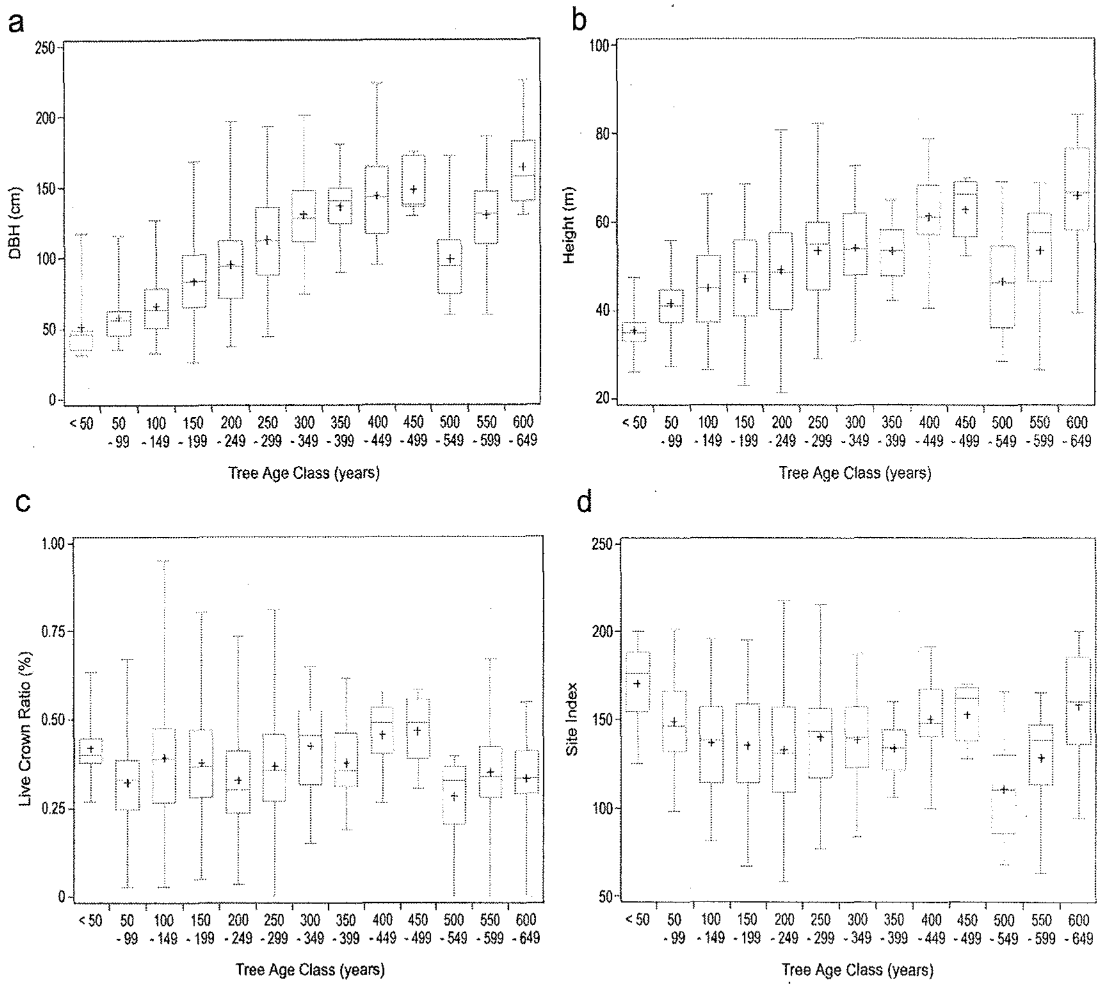


Figure 3. Box-and-whisker plots showing the relation of a) dbh, b) height, c) live crown ratio, and d) site index to tree age (50-yr classes) for 854 sample trees from the Douglas-fir section of the National Log Grade Project (DLGP). The bottom and the top of the box show the 25th and 75th percentile (lower and upper quartile, respectively), while the band near the middle is the median (50th percentile) and the cross (+) is the mean. The whiskers extend from the lower and upper quartiles to the extreme values (minimum, maximum) in the data.

sample areas. These trees formed a distinct group in plots of age vs. diameter or height, so box-and-whisker plots were constructed to examine the variation and trends. The influence ofthe 500-599 yr old sample trees on the relationship between tree age and DBH is shown in Figure 3a while the one between tree age and height is shown in Figure 3b. Log-transformations of the relations between age, dbh, height, and *H/D* ratio (In[age], In[dbh],, In[ht], and In[H/D], respectively) were done to meet parametric assumptions. Retaining the full data set, rather than grouping it, reflects an assumption that the DLGP sample is from a population of trees growing in average natural stand density conditions and undergoing natural stand development (mortality, self-thinning) across the Douglas-fir region.

## Data Analysis

I favored a simple approach to fitting equations to the data over approaches for developing predictive equations since some original field measurements were coarse (i.e., branch diameter classes) and others lacked precise definitions (i.e., live crown base). I used multiple linear regression to test relationships among tree, crown, and branch attributes, stand density and stand productivity by following the logic described in each section below.

Parsimonious regression equations with the fewest significant variables ($P<0.01$) were selected when $R^2$ values were marginally different ( <0.2) and AIC values were lower (see discussion in Burnham and Anderson [2004]). Results were checked for consistency against published dimensions of Douglas-fir trees from old-growth forests in the Cascade ranges of central Oregon (e.g., Pike et al. 1977, Massman 1982) and southwest Washington (Ishii and McDowell 2002).

*Tree-Published* models relating height to diameter include both parabolic (e.g., $H = a + bDBH - cDBH^2$) and linear forms, with log transformations of both variables (InH=a + b* (InD) or of just one (H=a+ b*InDBH) (e.g., Husch et al. 2003). The single transformation form (InDBH) was used for this analysis. It has been reported for Douglas-fir trees measured in old growth forests within the range of the historic DLGP data (Van Pelt and North 1996). Other potential explanatory variables introduced to explain the measured variation in tree height included tree age, In(age), site index, and stand basal area. The order reflects the assumption that while height growth of dominant trees is considered sensitive to site index, it is only weakly correlated with stand density (Davis and Johnson 1987). In contrast, the regression model for DBH tested In(age), tree height, basal area, and site index because diameter growth is strongly associated with density (as proxied by basal area). The last tree dimension of interest was *H/D* ratio. Because it has been used to predict tree susceptibility to storm damage, factors influencing this ratio are discussed in a literature on wind risk (e.g., Mitchell 2000); an inverse relationship to stand density is common. Furthermore, H/D ratio may be related directly to tree taper (Hasenauer and Monserud 1996). Since the oldest trees in old-growth forests have survived a range of competitive conditions and occupy the more open-grown conditions associated with density-independent mortality and non-uniform canopy structure, a trend of decreasing *H/D* ratio with tree age was assumed.

Crown-The crowns of open-grown trees generally cover a larger proportion of the stem than the crowns of trees growing in competitive conditions. The crown dimension of interest, LCR, could thus be expected to decrease progressively with forest closure and the corresponding death of (shaded) lower branches. The variance of LCR in the DLGP data, unlike in the Austrian data analyzed by Hasenauer and Monserud (1996), did not increase linearly with tree size or age (Figure 3c). Their logistic model form was, therefore, not adopted, but their potential explanatory factors were used as the starting point for multiple regression, with LCR modeled as a function of In(H/D), tree size (height and dbh), competition-density (basal area), and site condition (site index).

*Branches-Natural* pruning of branches in Douglas-fir trees occurs slowly because dead limbs are both decay-resistant and persistent (Kotok 1951). Nonetheless, their lower limbs would be expected to die with increasing stand density and tree age. Factors affecting the relative height of live and dead first branches and their size were anticipated to include tree size (height, dbh) and age, plus site and stand conditions. The preliminary data analyses had suggested that the variance of branch size (live and dead) increased with log transformations of either tree height or diameter. Given a lack of published equations for the diameter of first branches in Douglas-fir, an allometric model form was taken as a starting point. Relative branch height (both live and dead) was expected to be related to stand basal area, site index, and tree age.

## Predicting Branch Dimensions

The best-fitting branch equations were used to estimate tree and site effects on branch attributes of size and relative height. This was first done by calculating the mean predicted first live and dead branch diameter and the mean height to the first dead branch for a tree of fixed dbh (127cm) over a range of tree ages (100-600 yrs) and stand basal area (10-150$m^2$/ha) represented by the DLGP data. Next, expected differences in branch dimensions were further explored by fixing stand basal area and site index at approximately the DLGP mean (Table 1) and then varying tree diameter (80cm, 127cm and 250cm) and tree age (200 yr, 400 yr, 600 yr).

## Results and Discussion

Differences between old Douglas-fir trees and younger trees with the same dbh were revealed more strongly in the dimensions of their first

TABLE I. Summary statistics for sample Douglas-fir trees (n=854) harvested in Washington, Oregon, and California in the 1960s.

| Variable | Mean | Standard error | (Minimum, maximum) |
|---|---|---|---|
| **Tree** | | | |
| DBH (cm) | 98.3 | ±1.3 | (26.2, 225.5) |
| Height (H) (m) | 49.8 | ±0.4 | (21.3, 84.1) |
| Tree age (yr) | 252 | ±4.6 | (38, 647) |
| Height/Diameter (H/D) | 0.56 | ±0.01 | (0.19, 1.6) |
| Crown Base (CB) (m) | 31.8 | ±0.4 | (2.4, 67.1) |
| Crown Depth (H-CB) (m) | 18.1 | ±0.3 | (0, 54.9) |
| **Branch** | | | |
| Diameter of first dead branch (cm) | 3.0 | ±0.1 | (1.27, 15.2) |
| Diameter of first live branch (cm) | 5.7 | ±0.2 | (1.3, 50.8) |
| Height to first dead branch (m) | 9.7 | ±0.3 | (0, 43.98) |
| Height to first live branch (m) | 18.4 | ±0.3 | (0.45, 49.9) |
| **Stand** | | | |
| Basal area ($m^2$/ha) | 53.1 | ±0.9 | (2.7, 154.9) |

branches than in their crowns across the range of site indices and stand basal area represented by the DLGP sample (Table 2).

### Tree

The dimensions of sample trees used in this analysis were similar to those reported from other studies of old-growth Douglas-fir trees in the region. This is important, as it implies that the DLGP sample trees were like the trees being measured in more recent studies. For example, substituting the age (400 yr) and dbh (136 cm) of the tree sampled by Pike et al. (1977) into the equation for relative height of the first dead branch in this study (for an average stand basal area of 53.1) yields a prediction of 0.24. This compares to a value of 0.23 computed from published data on the original sample tree (Pike et al. 1977). For the size of the first live branch, substituting the tree age (415 yr) and diameter (135cm) of the tallest tree reported by Ishii and Ford (2001) into the equation for live branch diameter from this analysis (Table 2) yields a predicted size of 7.78 em. The branch diameter reported by Ishii and Ford (2001) for the lower crown (not necessarily the lowest, or first branch) was 8.4 cm.

Direct comparisons for other tree dimensions were limited by the availability of reported stand basal area and site index values. However, relations between dbh, age, and height were within the range of other published studies (Table 3). For example, substituting the height (62m) and age (415 yr) attributes of the tallest tree reported by Ishii and Kadotani (2006) into the dbh equation in Table 2 yields a dbh estimate of 129 cm compared to the measured 135.3 ern. Estimated tree heights were also within range when age and diameter data from Pike et al. (1977) were substituted into the equation (Table 2) for a range of basal area values. This is notable, as the DLGP sample trees aged 500-599 were harvested from areas with lower than average site index values (Figure 3d). The interaction of age and site cannot be tested due to limitations in the original data, but the dimensions of trees older than 500 years in the DLGP sample suggest an effect.

### Crown

The live crown ratio of the DLGP sample trees was characterized by variability across all age classes (Figure 3c). Evidence of age-related changes in live crown ratio was weak, with H/D ratio and stand basal area also contributing to the final equation (Table 2), which explained a minimal amount of the observed variation ($R^2$=0.11). Nonetheless, the range of LCR in the DLGP sample is similar to LCR for old-growth Douglas-fir trees other reported elsewhere. The six old-growth trees studied by Ishii et al. (2000) were compared to nineteen DLGP sample trees that also grew in Skamania County, Washington and were from a similarly aged stand (450 yr). The mean LCR of the former (0.64) is greater than the latter (0.45), but lies within the interval of the DLGP data for this age class (Figure 3d).

### Branches

Evidence for age-related differences in the mean diameter and the relative height of the first live and dead branch exist (e.g., Figure 4a). These differences were observed across the range of basal area, tree age, and dbh represented by the DLGP data set. Results suggest that the mean diameter of the first live branch was directly related to tree dbh. At a given age and stand basal area, larger-diameter trees had larger-diameter first live branches than those of smaller girth (Figure

TABLE 2. Multiple regression equations for Douglas-fir tree and branch attributes from data collected in Washington, Oregon, and California in the 1960s (n=854).

| Model | Parameter | Coefficient | SE | *P* | $R^2$ |
|---|---|---|---|---|---|
| **Tree** | | | | | |
| Total height | | | | | 0.96 |
| | intercept | -55,557 | 0.937 | 0.0001 | |
| | ln(dbh) | 2,079 | 0.373 | 0.0001 | |
| | ln(age) | 9,137 | 0.253 | 0.0001 | |
| | Basal Area | 0.010 | 0.003 | 0.0029 | |
| | site index | 0.336 | 0.004 | 0.0001 | |
| DBH | | | | | 0.72 |
| | intercept | -177.79 | 17,697 | 0.0001 | |
| | ln(age) | 33,889 | 3.24 | 0.0001 | |
| | height | 1,525 | 0.290 | 0.0001 | |
| | site index | 0.186 | 0.106 | 0.0782 | |
| | Basal Area | -0.15 | 0.029 | 0.0001 | |
| Height/diameter ratio | | | | | 0.45 |
| | intercept | 1,622 | 0.04 | 0.0001 | |
| | ln(age) | -0.196 | 0.008 | 0.0001 | |
| | Basal Area | 0.001 | 0.0002 | 0.0001 | |
| | site index | 0.0004 | 0.0001 | 0.0026 | |
| Live crown ratio | | | | | 0.11 |
| | intercept | 0.402 | 0.016 | 0.0001 | |
| | ln(HD) | -0.19 | 0.02 | 0.0001 | |
| | tree age | -0.0001 | 0.000 | 0.0026 | |
| | Basal Area | -0.001 | 0.0002 | 0.0001 | |
| **Branch** | | | | | |
| First live branch (dbh) | | | | | 0.35 |
| | intercept | 5.99 | 0.62 | <0.0001 | |
| | $dbh^2$ | 0.0002 | 0.00001 | <0.0001 | |
| | site index | -0.009 | 0.005 | 0.069 | |
| | $ta^2$ | 0.000009 | 0.00002 | 0.0001 | |
| | Basal Area | -0.044 | 0.0048 | 0.0001 | |
| First live branch relative HT | | | | | 0.12 |
| | intercept | 0.765 | 0.06 | <0.0001 | |
| | ln(dbh) | -0.165 | 0.018 | <0.0001 | |
| | tree age | 0.0004 | 0.00005 | 0.0001 | |
| | Basal Area | 0.0008 | 0.0002 | 0.0001 | |
| | site index | 0.0014 | 0.0002 | 0.0001 | |
| First dead branch (dbh) | | | | | 0.30 |
| | intercept | 2.23 | 0.148 | <0.0001 | |
| | $dbh^2$ | 0.000082 | 0.000008 | <0.0001 | |
| | $ta^2$ | 0.0000058 | 0.000007 | <0.0001 | |
| | Basal Area | -0.0118 | 0.0023 | <0.0001 | |
| First dead branch relative HT | | | | | 0.35 |
| | intercept | 0.299 | 0.50 | 0.0001 | |
| | tree age | 0.00075 | 0.00004 | <0.0001 | |
| | ln(dbh) | -0.0788 | 0.0125 | <0.0001 | |
| | Basal Area | 0.0010 | 0.00016 | <0.0001 | |

TABLE 3. Tree, branch, and stand attributes from published studies within the region covered by the sample tree data from the Douglas-fir section of the National Log Grade Project (DLGP).

| Attribute | Tree age (or position) | Location | Value | Source |
|---|---|---|---|---|
| **Tree** | | | | |
| Mean tree height | dominant | Wind River, WA | 52 m | Parker et al. 2004 |
| Tree height | 415 | Wind River | 61.6 m | Ishii & Ford 2001 |
| DBH | 415 | Wind River | 135.3 cm | Ishii & Ford 2001 |
| DBH | 410 | Wind River | 126.9 cm | Ishii & Kadotani 2006 |
| Tree height | 405 | Wind River | 50.8 m | Ishii & Ford 2001 |
| DBH | 405 | Wind River | 93.9 cm | Ishii & Ford 2001 |
| Live crown ratio | dominant | Priest River, ID | 0.59 | Monserud & Marshall 1999 |
| Tree height | 410 | Wind River | 61.0 m | Ishii & Kadotani 2006 |
| Tree height | 405 | Wind River | 53.8 m | Ishii & Kadotani 2006 |
| DBH | 405 | Wind River | 104.3 cm | Ishii & Kadotani 2006 |
| Tree height | 395 | Wind River | 51.3 m | Ishii & Kadotani 2006 |
| DBH | 395 | Wind River | 87.1 cm | Ishii & Kadotani 2006 |
| Mean tree height | | Wind River | 52 m | Shaw et al. 2004 |
| Mean dbh | | Wind River | 111 cm | Shaw et al. 2004 |
| **Branch** | | | | |
| Live branch diameter | 415 | Wind River | 8.4 cm | Ishii & Ford 2001 |
| Live branch diameter | 405 | Wind River | 7.8 cm | Ishii & Ford 2001 |
| **Stand** | | | | |
| Basal area | old growth | Wind River | 82.9 $m^2$/ha | Shaw et al. 2004 |

4a). Across the range of tree ages and stand basal area, the DLGP data suggest that older trees had larger-diameter first live branches than younger ones with the same dbh (Figure 4b). The mean diameter of the first live branch was larger on trees harvested from stands with lower basal area in comparison to trees taken from stands recorded as having higher density. Similarly, the mean diameter of the first dead branch (Figure 5a) was directly related to tree age and dbh. At a given age and stand basal area, larger-diameter trees had larger-diameter first dead branches than did trees of smaller diameter (Figure 5b).

The pattern of older trees having larger diameter branches than younger trees of the same diameter held across a range of stand basal area. On average, the older a tree the larger were its first branches and the longer was its branch-free stem length. These results are consistent with processes of branch growth and death and the subsequent formation and overgrowth of knots. Between tree ages 200-600 yr, for example, results indicate that when basal area was fixed at 57 $m^2$/ha, the mean diameter of the first live branch was predicted to increase by half (Figure 4a). Likewise, mean live branch size in a 400 yr old tree harvested at basal area 28$m^2$/ha was about twice that of similarly aged tree harvested at basal area 114$m^2$/ha (Figure 4b). These results suggest that large (127cm dbh) young trees (e.g., 200 yr) had not yet developed the branch dimensions of older trees (e.g., 500 yr) with the same dbh. They support the speculation of Ishii and McDowell (2002) that branch growth and death are important processes in crown development of Douglas-fir.

The relative height of the first dead branch increased with tree age and with stand basal area (Figure 6a). Trees with smaller dbh had a higher relative branch height than larger diameter trees of the same age at a fixed basal area (Figure 6b). These ratios are consistent with the relationship of site index to tree height and diameter growth; a taller tree (older) would have a lower relative height of the first dead branch than a tree that was not as tall (younger) (for a visual image of relative branch height see Figure 2 in Van Pelt and Nadkarni [2004]).

The insights offered by the DLGP data shift according to the attribute offocus, with branches- and how their size and location relates to tree age-being the most important. Although a positive relationship with age is evident, the explanatory

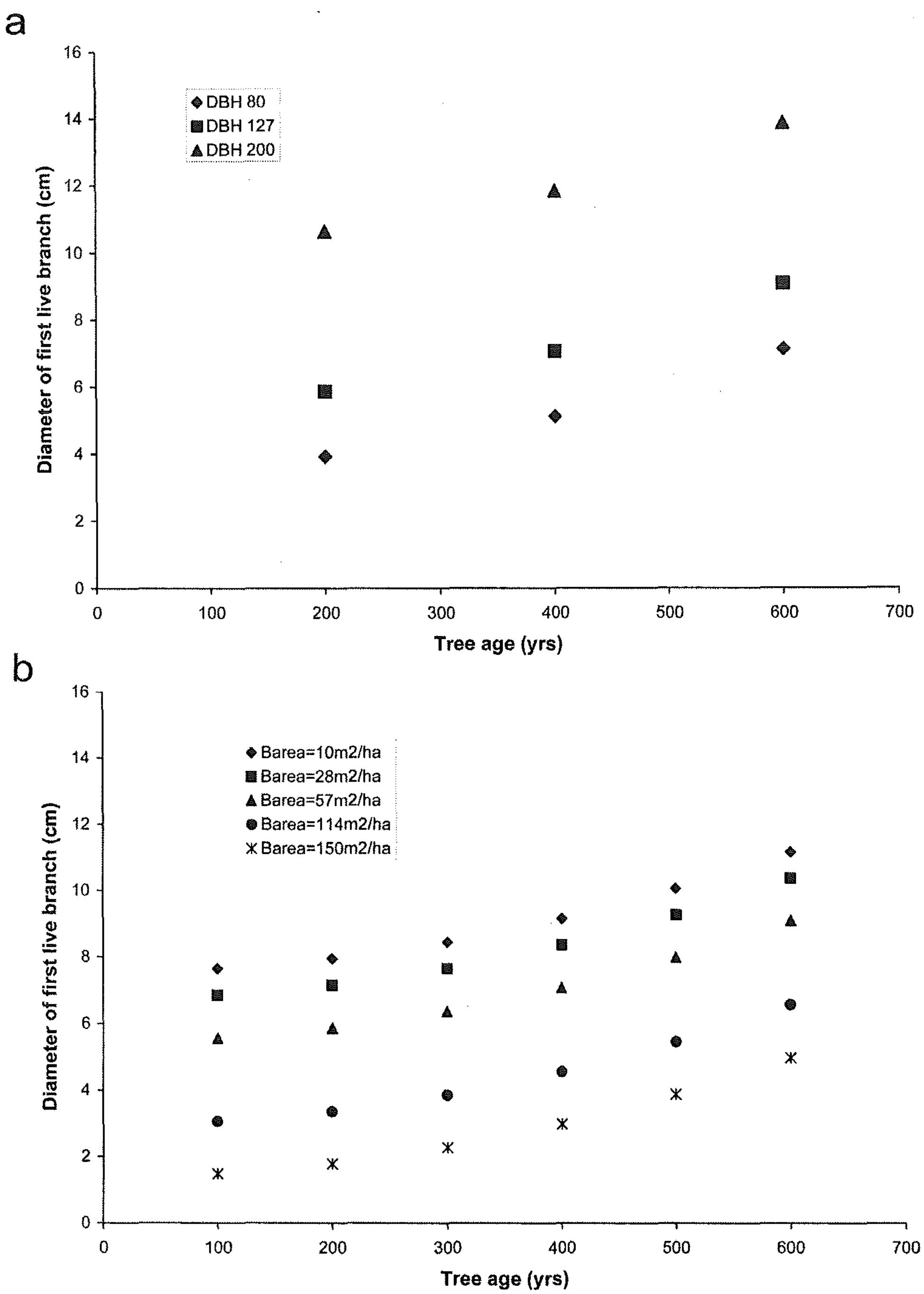


Figure 4. Mean diameter of the first live branch for trees (a) with different dbh (80, 127,200 cm) and age (200, 400, 600 yr) and (b) Mean diameter of the first live branch for trees aged 100-650 yr associated with different stand basal area (l0-150m$^2$/ha).

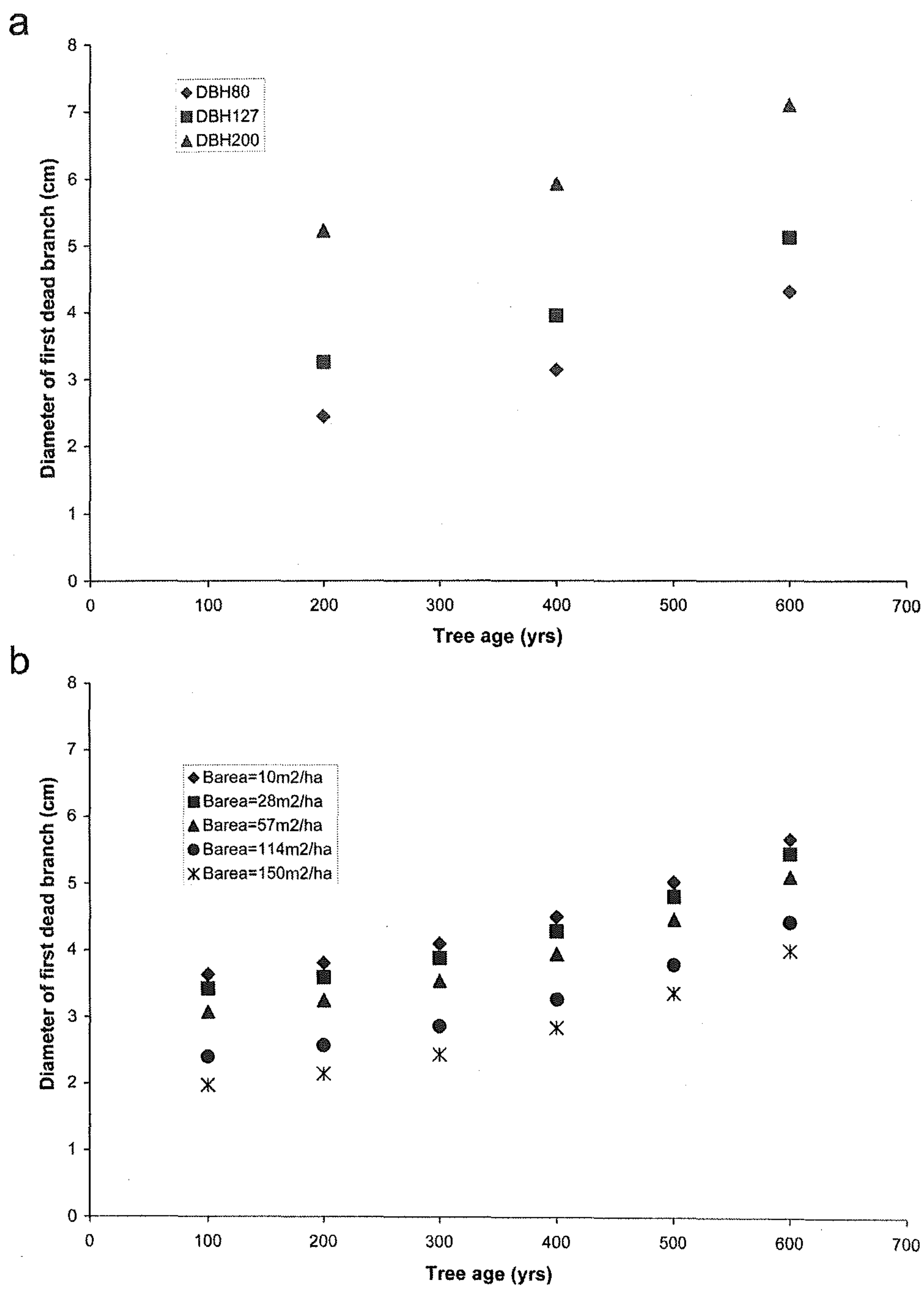


Figure 5. Mean diameter of the first dead branch for trees with (a) different dbh (80, 127,200 cm) and age (200,400, 600 yr) and (b) Mean diameter of the first dead branch for trees aged 100-650 yr associated with different stand basal area (10-150m$^2$/ha).

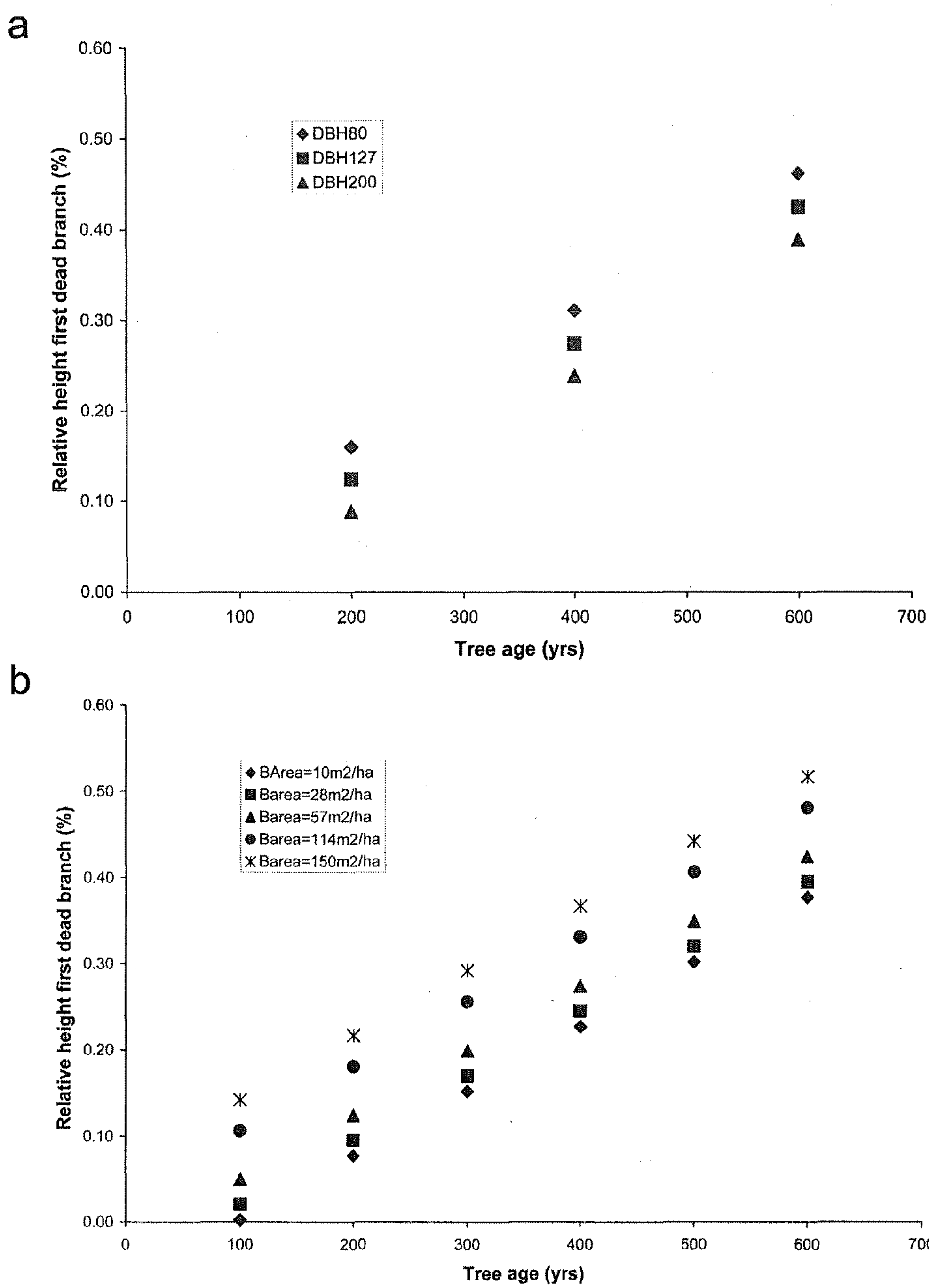


Figure 6. Relative height of the first dead branch for trees (a) with different dbh (80, 127,200 cm) and age (200, 400, 600 yr) and (b) Relative height of the first dead branch for trees aged 100-650 yr associated with different stand basal area (l0-150$m^2$/ha).

power of the branch models remains modest. For crowns the significance of tree age is minimal, but at the same time the variability in live crown ratio across the range of ages is notable. For trees, the equations for size confirm widely held assumptions about the influence of stand attributes; namely that height is only weakly correlated with density while dbh is negatively related to it. Study results suggest questions about relationships among tree longevity, tree size, and site productivity that are not answerable with the DLGP data alone.

The limitations imposed by an incomplete knowledge of DLGP study details and stand histories minimize the contribution of this paper to a growing literature on tree architecture in old-growth forests dominated by Douglas-fir. Study results reinforce rather than contradict existing knowledge. Nonetheless, the vintage of the DLGP data, which could be seen as a constraint on their usefulness, is also a source of their value. Today it would be unthinkable to harvest the number of trees in the DLGP sample, yet the variability measured in the historical data set underscores the importance of avoiding small samples from a limited number of places when drawing inferences about the crown architecture of Douglas-fir trees.

The variability in LCR observed in the DLGP sample is documented in other published reports in both coastal (Spies et al. 1990, Temesgen et al. 2005) and interior (Brown 1978) old growth Douglas-fir forests. The lack of clear signs of age-related differences in LCR could be explained by processes of branch death, the development of epicormic branches in the absence of trauma (Lanner 2002) and the redistribution of branch volume with tree age (Massman 1982, Ishii and Ford 2001). A LCR that varies little over time has been postulated to confer stability (Van Pelt and Nadkarni 2004) and longevity (Lanner 2002). Contributing factors could be the accretion and abrasion of branches (Putz et al. 1984) combined with the natural sway frequencies and damping ratios of trees (Moore and Maguire 2004). Ishii and McDowell (2002) also proposed that branch death occurs higher in the crown for old stands than for young ones. Although limited to the characteristics of the first live and dead branch, this study offers some support for this proposal. It remains unclear if controls on these changes are primarily tree level (i.e., physiological) or population level (i.e., competitive) (Smith and Long 2001).

That some of the oldest trees (>500 yr) had smaller mean diameters than some younger trees could be related to sample selection. The oldest trees harvested were generally from sites with lower than average site index values, perhaps because similarly aged trees on more productive sites exhibited rot or other defects exceeding the sampling and milling standards. The "relatively short and small" stature of Douglas-fir in a 500-year-old stand on a lower productivity site was also noted by Van Pelt and Nadkarni (2004), however the effect of site productivity on longevity lies outside the scope of the DLGP data.

The variability measured in the DLGP sample trees is important, particularly given the development of forest growth models after the DLGP data were collected. In the Douglas-fir region, models are used to simulate changes in tree or forest structure and wood quality associated with contemporary silvicultural treatments (Barbour et al. 1997). Because growth is related to foliage biomass and its distribution, single-tree models often include crown size as a predictor of height or diameter increment and mortality. Crown size is sometimes estimated by using allometric relations derived from tree size and stand density data (Hasenauer and Monserud 1996). The ratio of live crown length to tree height (live crown ratio) is also included as an indicator of vigor (Temesgen et al. 2005) or a predictor of basal area increment (Hasenauer and Monserud 1996). Species-specific tree and crown data over a range of tree ages and growing conditions are vital for developing and using allometric equations, which can in turn have other uses. For example, the structural attributes of Douglas-fir crowns and branches have been used as a proxy for other variables that are difficult to measure like leaf area or sapwood area (Turner et al. 2000). Models often lack branch data (Busing and Garman 2002) or rely on branch data collected on trees from second-growth forests (Garman 2004). Published branch studies typically reflect a focus on wood quality and rely on sampling young (<100 yr) or plantation-grown trees (e.g., Maguire et al. 1999). Predicting the structural development of forests in the Douglas-fir region and the effects of silvicultural practices like pruning or thinning on tree and wood characteristics requires caution when conditions lie outside the data used in model development.

This paper reflects the flaws and opportunities of using inherited data. The significance of study results is hampered by a lack of certainty about data collection methods, which carries over into limits in statistical testing to investigate hypotheses. Furthermore, since chronosequences cannot identify cause and effect, the age-cross section represented in the **DLGP** data must be accepted as a valid surrogate for a time series. Given these limitations, study results contribute to contemporary discussions of managing structural complexity in second-growth forests. They provide modest evidence of differences between the size and location of branches on old trees or on younger trees with the same diameter on sites spanning a range of average natural stand density conditions within the Douglas-fir region.


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