Branch growth and crown form in old coastal Douglas-fir

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Abstract

Theoretical and empirical methods were applied to the analysis of branch growth and crown form in old trees of coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*). Conventional use of allometric models proved insufficient in explaining the variability found in the relationship between branch diameter and length. In order to infer the potential pattern of branch growth, a maximum relationship was empirically estimated by selecting maximum points in an incremental fashion. This relationship asymptoted to infinity, suggesting that factors such as damage and die-back may modify the branch diameter–length relationship before an asymptotic maximum length is reached. The difference between the observed branch length and the estimated maximum branch length was found to be a good measure of the degree of branch damage. The degree of damage increased with increasing branch diameter, suggesting that large diameter branches have experienced more extensive damage and/or die-back. This trend was stronger in dead branches than in live branches. A conceptual model of branch growth is proposed where damage and die-back modify the branch diameter–length relationship, severe damage and die-back lead to branch death, and recovery helps to restore the relationship in live branches. The vertical distribution of branch diameters within the crown was analyzed to characterize crown form. An allometric model describing the maximum relationship between branch height and branch diameter was fit to each tree. Two types of distribution patterns were identified: the *conical* and *rounded*. The frequency distributions of branch diameters at three crown levels (upper, mid and lower crown) were also used to characterize crown form. Three crown types were characterized: the *mature crown*, *old crown*, and *stressed crown*. These crown types corresponded well with the vertical distribution patterns of maximum branch diameters. The two criteria are suggested as a useful tool for characterizing crown form in old coastal Douglas-fir for purposes of forest management. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Branch growth; Crown form; Allometry; Old trees; Coastal Douglas-fir

1. Introduction

The relative growth and form of trees has interested plant morphologists and ecologists for several decades. Various theoretical and empirical relationships among tree dimensions have been discovered and their

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ecological and evolutionary significance discussed. Among these, allometric relationships have been frequently used to infer patterns of tree growth and form (Niklas, 1994). Although there has been some criticism of the use of allometric relationships (Smith, 1980), it still remains an effective method for describing scaling relationships among morphological traits in both plants and animals (Bertram, 1989). Theoretical explanations for the various allometric relationships have been proposed, some of which are based on mechanical properties. For example, the 'mechanical design of trees' (MacMahon and Kronauer, 1976) has been studied in detail, and various mechanical models have been proposed to explain tree structure (Niklas, 1993).

However, most theoretical relationships on tree structure are based on measurements taken from young to mature trees. Old trees, some of which can be over 300-years-old, present an excellent opportunity to explore whether or not such relationships can endure the test of time and environmental factors that may work to modify the relationships. Understanding the growth and development of old trees is important for ecological studies of natural stands. In addition, recent interest in ecological management of old natural forests calls for further study of older trees.

In this study, we applied theoretical and empirical methods to analyze branch growth and crown form in old trees of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) to test whether their structure conformed to the structural models derived from younger trees.

1.1. Branch growth

Previous research has shown that there is an allometric relationship between branch diameter and length (MacMahon and Kronauer, 1976; Bertram, 1989):

$$L = a D^b \qquad (1)$$

where L is branch length, D is branch diameter, a is a coefficient, and b is the scaling exponent. In addition, it has been suggested that the taper in branch diameter should be such that at any given point on a branch, the relationship between the diameter at that point (D_i)

and the branch length beyond that point (L_i) can be written:

$$L_i + L_0 = a D_i^b \qquad (2)$$

where L_0 is the distance from the actual branch tip to the 'virtual tip' where branch diameter equals 0. Based on this 'tapered cantilever beam' model, MacMahon and Kronauer (1976) found that $b \cong 0.667$ using measurements from several branches on single trees, and discovered that branch dimensions conformed to 'elastic similarity.' However, the estimation method used by MacMahon and Kronauer (1976) assumes that L_0 is constant across all branches. This assumption may be valid for young trees where most branches are intact. However, in old trees, branches may have suffered damage, die-back and subsequent recovery during the long life-span of the tree, adding variability to the relationship between branch diameter and length, and L_0 is likely to vary from branch to branch. Therefore, Eq. (2) must be fit to each branch individually, using multiple diameter and length measurements from the same branch (Fig. 1). It is then, theoretically possible to estimate L_0 for each branch using Eq. (2) to assess the degree of branch damage. In this study, we assess the application of the tapered cantilever beam model as a method for estimating the degree of branch damage in old trees of coastal Douglas-fir.
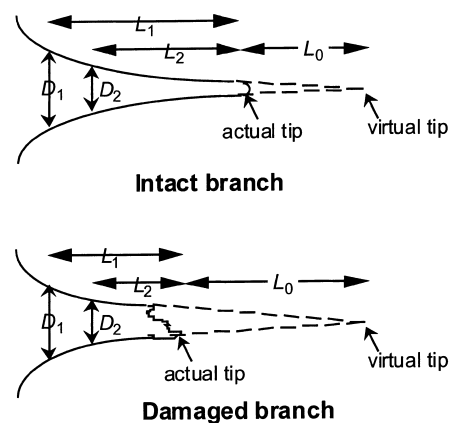

Fig. 1. The theoretical relationship between branch diameter and branch length in intact and damaged branches. Multiple measurements of branch diameter and length may be used to estimate the degree of branch damage.

In addition to their variable growth history, branches have multiple functions other than that of mechanical support, including water transport and storage of photosynthate. Mechanical models alone may not be sufficient to explain the relationship between branch diameter and length, nor to estimate degrees of branch damage in old trees. We also explored empirical methods for estimating the degree of branch damage, and inferred patterns of branch growth.

1.2. Crown form

Allometric relationships have also been used to describe crown form (Nepal et al., 1996). Studies of crown form have provided useful information on patterns of crown development and their implications for production in coniferous stands (Fujimori and Whitehead, 1986; Oker-Blom and Kellomaki, 1987). It is known that branch length and diameter varies with depth-into-crown, reflecting the age and growth pattern of branches at various crown levels. The vertical distribution of branch diameters has been used to estimate the vertical distribution of foliage within the crown of young trees (Maguire and Bennett, 1996; Gilmore and Seymour, 1997). Studies on young coniferous trees have found increasing branch diameter down the crown with a slight decrease in the lower crown (Colin and Houllier, 1992; Maguire et al., 1994; Gilmore and Seymour, 1997; Roeh and Maguire, 1997). However, measurements in old trees have shown considerable variability in the vertical distribution of branch diameters both within and among trees (Massman, 1981).

As trees get older, branch death occurs, and crown form may be modified (Maguire and Hann, 1987; Kershaw et al., 1990). In coastal Douglas-fir, epicormic branches originating from the main stem often grow to replace dead or dying branches, especially in the lower crown (Franklin et al., 1981). Branch death and growth of epicormic branches adds variability to the vertical distribution of branch sizes within the crown. The rate at which these changes in crown form occur may differ among individual trees depending on the local environment, adding to the variability in crown form among old trees. In this study, we investigate the vertical distribution of branch diameters within the crowns

of old trees of coastal Douglas-fir and infer patterns of crown development.

2. Study site and methods

The study was conducted in a 450–500-year-old coastal Douglas-fir -western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forest at the Pacific Crest Area along Trout Creek, in the Wind River Ranger District, Gifford Pinchot National Forest, southwestern Washington State, USA. The stand is dominated by coastal Douglas-fir and western hemlock followed by western red cedar (*Thuja plicata* Donn ex D. Don), Pacific silver fir (*Abies amabilis*. Dougl. ex Forbes) and Pacific yew (*Taxus brevifolia* Nutt.). Other tree species in the stand include: grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), western white pine (*Pinus monticola* Dougl. ex D. Don), and Pacific dogwood (*Cornus nutilii* Audubon). See Franklin (1972) and Franklin and DeBell (1988) for a description of the area.

Nine old coastal Douglas-fir trees were selected for measurement of crown characteristics. All trees were growing in an open riparian area and had emergent and isolated crowns relative to the surrounding canopy. The trees are believed to have established after a stand-replacing major disturbance in the area, and are likely to be 230–460-years-old (Franklin and DeBell, 1988). The crown of each tree was investigated using single-rope climbing techniques (Perry, 1978; Moffett and Lowman, 1995). The diameter at the base of each branch was measured immediately outside the branch collar using diameter tape. Branch height off the ground was measured using a tape measure that was stretched vertically along the main stem of the tree. Branch length was measured for a randomly selected sub-sample of 10% of the total number of branches in each tree using an extending measuring pole. Of these, diameter at branch tip was also measured for the dead branches. Measurements on branches in the upper 2–3 m of each tree were avoided due to safety reasons. Twenty-five live branches of various diameters were selected from the sub-sample for measurement of diameter taper along the branch and the slope of the branch at 0.5, 1.5, 2.5 and 3.5 m out from the main stem, using diameter tape and clinometer, respectively. Further measure-

ments out on the branch were avoided for safety reasons.

2.1. Branch growth

Eq. (2) was fit to the series of diameter and length measurements from each of the 25 live branches sampled for diameter taper using nonlinear least-squares regression. To reduce the effect of compensation among the parameters, elastic similarity was assumed ($b = 0.667$), and only L_0 and a were estimated. L_0 was not restricted to positive values so as to obtain an unbiased estimate. The estimates were used to assess whether these branches conformed to the elastically similar tapered cantilever beam model.

The overall relationship between branch diameter and length was explored using nonlinear least-squares fits of Eq. (1) to all live branches. Branches from all nine trees were pooled to investigate the general growth pattern of branches in old, isolated crowns of coastal Douglas-fir.

Eq. (1) describes a simple allometric relationship where branch length increases with branch diameter. However, it is unlikely that branch elongation will continue indefinitely, either due to repeated damage, die-back, or internal control, and an asymptotic maximum branch length may be reached. The exponential generalization of the allometric equation, which describes an asymptotic relationship, was also fit to all live branches:

$$L = L_{max}(1 - \exp(k D^c)) \tag{3}$$

where, L_{max} is the asymptotic maximum branch length, k is a coefficient, and c is the scaling exponent. This equation has been used to describe tree diameter–height relationships, e.g., Thomas (1996).

Because branches of old trees have been modified by factors such as damage, die-back and subsequent recovery during their long life-span, we also developed an empirical method for estimating the potential pattern of branch growth in old trees. In order to empirically estimate the potential pattern of branch growth, a maximum relationship should be fit to data from all branches (live and dead). Various techniques have been suggested for estimating maximum relationships. Osawa and Sugita (1989) used a number of the outer most data points to define the upper bounds of the self-thinning relationship. Webb (1972) pro-

posed the 'boundary-line analysis', where data are divided into size classes based on the independent variable, and maximum dependent variable values are chosen in each size class to define the 'boundary-line.' Others have proposed visually estimating the boundary line that 'enclose(s) the uppermost observations with a smooth curve' (Chambers et al., 1985). Nepal et al. (1996) used a stochastic frontier model, where residuals are restricted to negative values, to fit maximum relationships to crown profile data. Both Osawa's method and boundary-line analysis involve arbitrary decisions in choosing the maximum points and size classes. The stochastic frontier method is technically involved and is still in its developmental stages for application to forestry. Here, we chose the set of maximum points in an incremental fashion. Under the assumption that maximum branch length should increase with increasing branch diameter, increasingly larger branch lengths were chosen with increasing diameter, while lengths smaller than the previous maximum were ignored. This method may still be insufficient for estimating the maximum relationship if the selected set of maximum points do not show a good relationship. Eqs. (1) and (3) were fit to the maximum points to test this. A good fit of the allometric relationship would define the empirically estimated maximum branch length for a given diameter. The difference between the observed and estimated maximum branch length could then be interpreted as the degree of branch damage and compared between live and dead branches to infer the pattern of branch growth and death.

2.2. Crown form

The vertical distribution of branch diameters in each tree was explored through analysis of the relationship between branch height and branch diameter. Due to the high variability, a mean relationship describing the vertical distribution of all live branch diameters proved difficult to fit. Instead, a maximum relationship was fit to each tree using the set of maximum points selected from all live and dead branches following the same method used to estimate maximum branch length. Maximum points were selected from the top of the crown toward the bottom and again from the bottom of the crown toward the top until the maximum branch diameter in the tree was reached. The allo-

metric equation proposed by Nepal et al. (1996) to describe crown form was fit to this set of maximum points:

$$D = p\, d^q (1 - d)^r \tag{4}$$

where, D is the branch diameter, d is relative depth-into-crown, p is a coefficient, and q and r are the scaling exponents.

$$d = \frac{\text{tree height} - \text{branch height}}{\text{crown depth}}$$

where,

crown depth = tree height − lowest branch height.

In addition to the above model, the frequency distributions of branch diameters at three crown levels (upper, mid and lower crown) were examined to characterize crown form qualitatively. The crown of each tree was divided into three equal levels based on the relative depth-into-crown, and the frequency distributions of diameters of both live and dead branches were calculated for each crown level.

3. Results and discussion

3.1. Branch growth

Of the 25 live branches sampled for diameter taper measurement, nine yielded negative estimates of L_0, and only six had $r^2 > 0.9$ (Table 1). In addition, the slopes of these branches were highly variable, both within and among branches, suggesting that the elastically similar tapered cantilever beam model may not be applicable to branches of old coastal Douglas-fir, and Eq. (2) can not be applied to estimate the degree of branch damage. Although other studies have presented more versatile versions of the tapered cantilever beam model (Morgan and Cannell, 1987), mechanical models alone may not be sufficient to explain branch

Table 1
Results of the nonlinear least-squares regression fits of the elastically similar tapered cantilever beam model. Branches are arranged in order of decreasing diameter

| Diameter (cm)	Length (m)	Height (m)	Mean slope ± s.d. (degrees)	a	L_0 (m)	r^2
40.0	9.0	27.8	1.25 ± 11.09	0.0267	−3.17	0.971
37.0	8.0	38.3	30.00 ± 5.00	0.0234	−1.84	0.886
33.0	8.0	27.1	−1.25 ± 10.31	0.0177	−1.15	0.877
31.8	6.0	35.5	23.33 ± 16.07	0.0307	−1.29	0.936
27.0	7.0	38.2	48.75 ± 23.94	0.0073	3.47	0.841
26.2	8.0	38.0	15.00 ± 8.66	0.0212	−2.48	0.879
25.0	7.0	34.6	8.33 ± 2.89	0.0187	−2.08	0.627
23.0	7.0	38.6	1.67 ± 7.64	0.0030	10.96	0.584
22.8	12.0	22.3	48.75 ± 9.46	0.0035	5.00	0.826
22.8	6.5	54.0	−58.33 ± 34.03	0.0170	−1.21	0.889
22.0	7.5	26.0	16.25 ± 8.54	0.0068	2.54	0.857
22.0	8.8	28.9	56.67 ± 16.07	0.0035	6.44	0.722
22.0	5.5	52.3	−21.67 ± 28.43	0.0146	0.16	0.836
21.2	7.5	36.9	28.33 ± 7.64	0.0146	−1.52	0.955
20.9	7.5	37.0	33.25 ± 5.68	0.0044	5.16	0.830
19.8	7.0	33.8	38.33 ± 11.55	0.0044	5.02	0.732
19.6	6.0	41.6	15.00 ± 13.23	0.0036	7.95	0.836
19.5	7.3	35.1	40.50 ± 3.32	0.0026	10.02	0.740
18.8	7.5	36.6	36.67 ± 2.89	0.0104	−0.59	0.964
18.1	10.0	19.4	−17.50 ± 8.66	0.0049	0.57	0.898
16.1	8.0	32.5	36.67 ± 2.89	0.0039	3.61	0.856
16.0	5.8	43.5	15.00 ± 8.66	0.0057	3.72	0.797
15.5	9.0	22.4	41.67 ± 10.41	0.0040	2.38	0.948
12.0	8.5	26.4	40.00 ± 5.00	0.0020	6.49	0.980
11.7	6.0	43.4	6.67 ± 2.89	0.0046	2.64	0.907
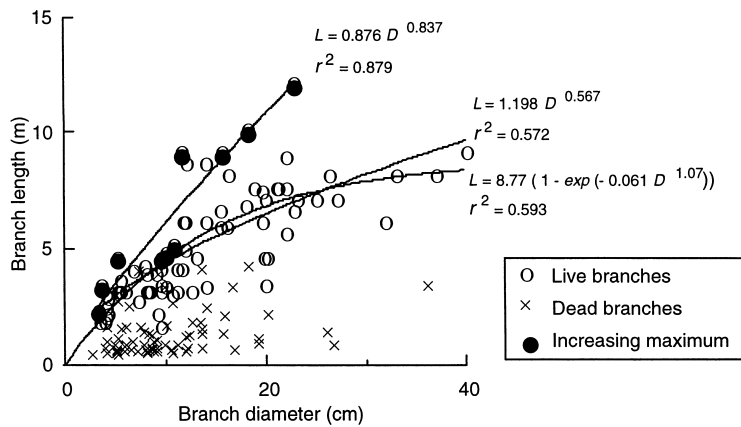
Fig. 2. The relationship between branch diameter and length in old coastal Douglas-fir. Both simple and asymptotic allometric relationships were fit to all live branches (O) and to the selected set of maximum points (●) using nonlinear least-squares regression.

structure in old trees. As branches have multiple functions other than that of mechanical support, and branch dimensions may have been altered by external factors, empirical methods may provide more insight into inferring the pattern of branch growth in old trees.

The mean relationships between branch diameter and length obtained by fitting Eqs. (1) and (3) to all live branches explained only 0.572 and 0.593 of the total variation, respectively (Fig. 2). The relationship obtained from Eq. (3) yielded an asymptotic maximum branch length estimate (L_{max}) of 8.77 m, which was shorter than the maximum observed branch length. This poor fit resulted from the high variability found in branch lengths.

The nonlinear least-squares fit of Eq. (1) to the set of maximum points yielded a good fit with 0.879 of variation explained. The good fit of Eq. (1) suggested that the selected set of maximum points are a good representation of the potential pattern of branch growth. The estimate of the scaling exponent, b, was 0.837 suggesting that the potential pattern of branch growth in old trees of coastal Douglas-fir may not conform to elastic similarity. The nonlinear least-squares fit of Eq. (3) to the set of maximum points asymptoted to infinity, suggesting that factors such as damage, die-back and branch death may modify the branch diameter–length relationship before an asymptotic maximum length is reached. Aiba and Kohyama (1996) found similar effects of mortality on estimates of maximum tree height in

tropical trees, where mortality of larger trees caused estimates of maximum tree height to be much larger than the observed maximum tree height.

The diameter–length relationship of dead branches was more variable than in the live branches. Many dead branches were found to be considerably shorter than the live branches for a given diameter. As live branches have the ability to recover after damage or die-back, they may be able to regain branch length, reducing the amount of variability found in branch lengths relative to dead branches.

The difference between the observed and maximum branch length of dead branches was strongly positively correlated with diameter at branch tip (Fig. 3, Spearman's rank correlation coefficient: $r_s = 0.694$, $n = 72$, $P < 0.01$), indicating that this was a good measure of the degree of branch damage. Increasingly larger differences between the observed and maximum branch lengths were found with increasing branch diameter indicating that, as branches get larger, their lengths tended to be increasingly shorter than the estimated maximum length (Fig. 4(a)). This may be the result of severe or repeated damage or die-back that larger branches may have suffered during their long life-span. This trend was stronger for dead branches than for live, suggesting that those branches that died were more extensively damaged, or that further damage may have occurred after branch death. Most live branches were less than 3 m shorter than the estimated maximum length, while most dead branches were 3–7 m shorter (Fig. 4(b)).
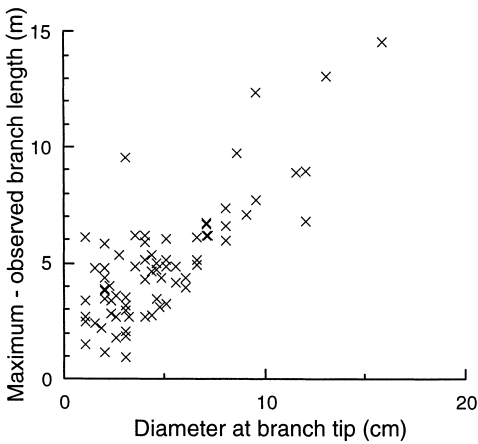
Fig. 3. The difference between the observed and maximum branch length of dead branches was strongly positively correlated with diameter at branch tip indicating that this was a good measure of the degree of branch damage.
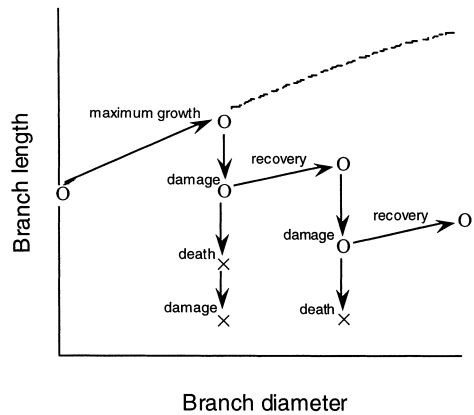
Based on these results, we propose a conceptual model of branch growth in old trees of coastal Douglas-fir (Fig. 5). A branch is expected to grow following the maximum diameter–length relationship until damage or die-back occurs. This modifies the branch diameter–length relationship, making the branch shorter than expected for its diameter. Subsequently, the branch may recover, or die if extensively or repeatedly damaged. Damage and die-back add variability to the branch diameter–length relationship.

Fig. 5. A conceptual model of branch growth in old coastal Douglas-fir. A branch is expected to grow following the maximum diameter–length relationship until damage or die-back occurs. This modifies the branch diameter–length relationship, making the branch shorter than expected for its diameter. Subsequently, the branch may recover or may die if extensively or repeatedly damaged. Damage and die-back add variability to the branch diameter–length relationship. However, recovery would work to reduce this variability in the live branches.

However, recovery would reduce this variability in live branches.

3.2. Crown form

The relationship between branch height and branch diameter was highly variable within and among trees
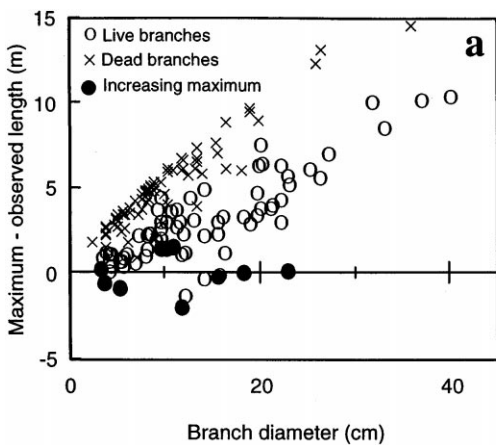

Fig. 4. The difference between the observed and maximum branch length increased with increasing branch diameter indicating that large diameter branches had experienced more extensive damage and/or die-back (a). This trend was stronger in dead branches ($\times$) than in live (O). Frequency distributions of the difference between the observed and maximum branch length showed that the degree of damage in most live branches (shaded bars) was less than 3 m while in dead branches (open bars) it ranged from 3 to 7 m (b).
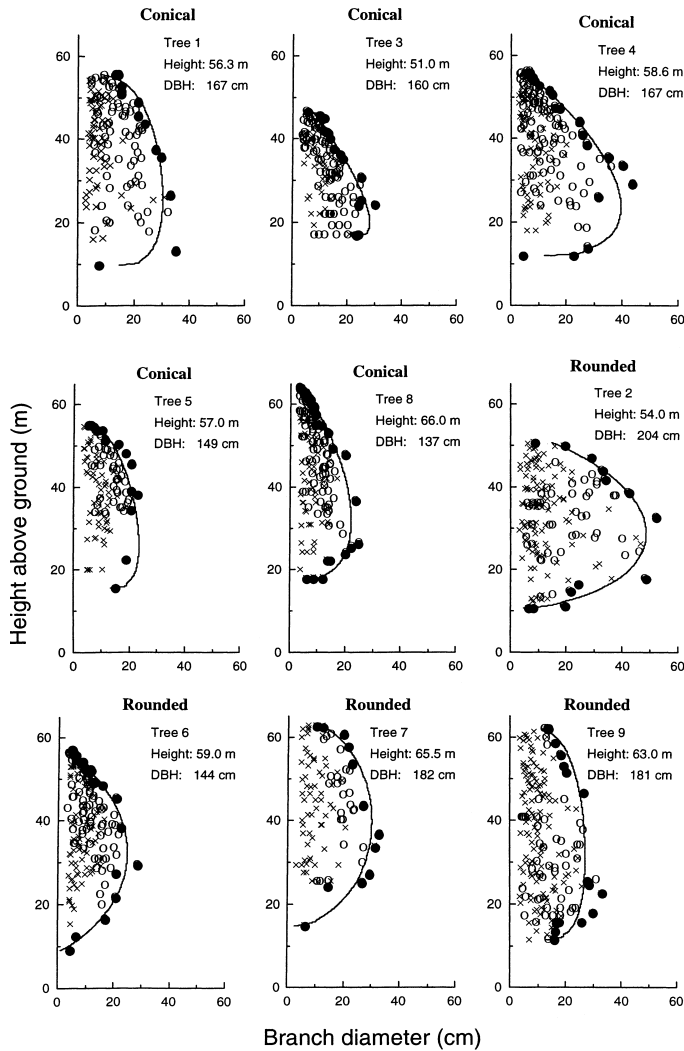
Fig. 6. Vertical distributions of branch diameters within the crowns of old coastal Douglas-fir (O: live branches, ×: dead branches) with nonlinear least-squares regression fits of an allometric crown profile model to the selected set of maximum points (●). Two types of distributions were identified: the conical distribution and the rounded distribution.

(Fig. 6). In all trees, the variance in branch diameters tended to be greatest near the height of the maximum branch diameter. The nonlinear least-squares fits of Eq. (4) to the set of maximum of points yielded good fits in most trees ($r^2 = 0.806$–0.940), except for Tree 1 ($r^2 = 0.695$) and Tree 9 ($r^2 = 0.597$). Two types of distribution patterns were identified. Trees 1, 3, 4, 5 and 8 showed the *conical* distribution pattern where the regression curve showed a conical form, and the maximum estimated branch diameter is reached

toward the lower crown, similar to distributions found in younger trees. Trees 2, 6, 7 and 9 showed the *rounded* distribution pattern where the regression curve showed a semi-ellipsoid form, and the maximum estimated branch diameter is reached near the middle of the crown.

The frequency distributions of branch diameters at the three crown levels were also variable (Fig. 7). However, trees could be characterized into three crown types: the *mature crown* type, where increas-
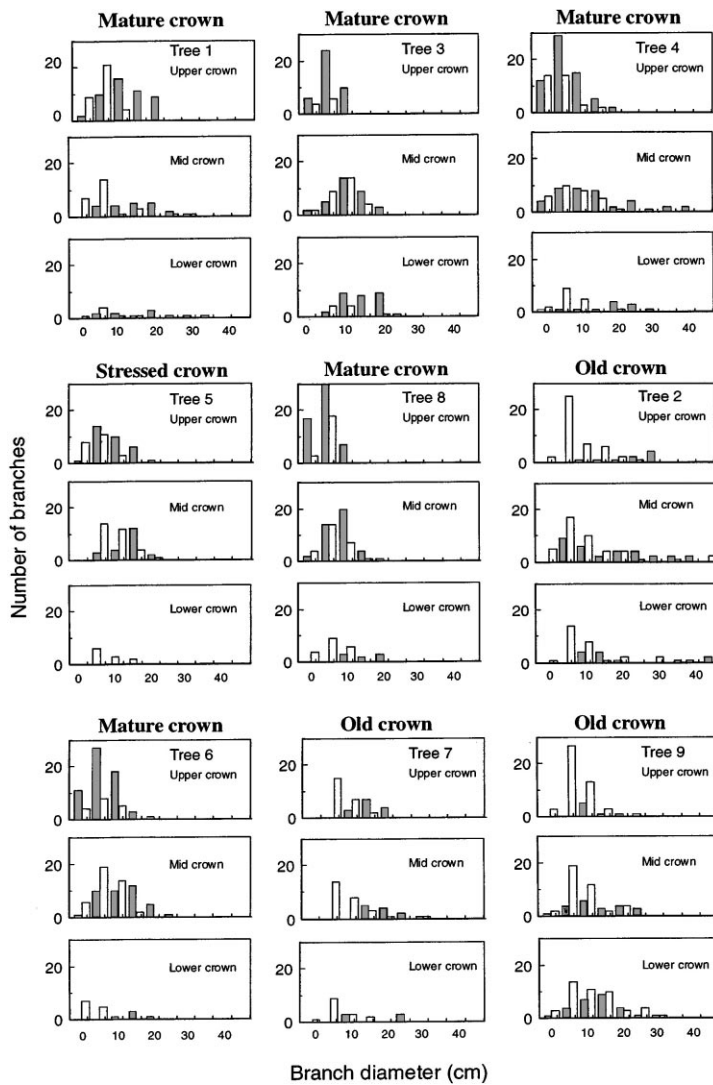
Fig. 7. Frequency distributions of branch diameters at three crown levels. Trees were characterized into three crown types: *mature crown*, *old crown*, and *stressed crown*, based on the shape of the distributions and the relative number of live (shaded bars) and dead (open bars) branches within the crown.

ingly wider range of live branch diameters are found toward the lower crown, while the diameter distribution of the dead branches remains relatively constant (Trees 1, 3, 4, 6, and 8); the *old crown* type, where the crown consists of a few large-diameter live branches, and many dead branches (Trees 2, 7, and 9); and the *stressed crown* type, where branch diameters are relatively small and there are very few, if any, live branches in the lower crown (Tree 5).

The vertical distribution patterns of maximum branch diameter corresponded well with the three crown types, suggesting that the two criteria may be useful in characterizing crowns of old coastal Douglas-fir. Trees with a conical distribution pattern of maximum branch diameters, with increasingly larger and presumably older branches toward the lower crown, corresponded to the 'mature crown' type (Fig. 8). As trees get older, branches in the upper
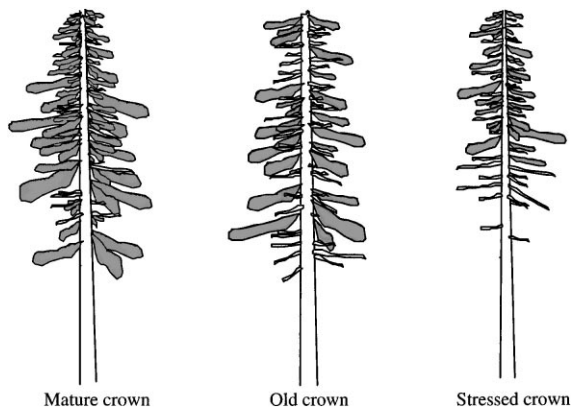
Fig. 8. A schematic diagram of typical trees of the three crown types.

crown increase in diameter, resulting in the rounded distribution of maximum branch diameters. Dead branches would accumulate in the crown, and the live crown would consist of a few old, large-diameter branches, resulting in the old crown type. Some trees may be affected by stresses, such as herbivore outbreaks or pathogens, as was the case for Tree 5 in this study. Branch growth in these trees is likely to be suppressed, and crown depth may be limited, resulting in the stressed crown type.

4. Conclusions

Our results suggested that branches of old coastal Douglas-fir trees have experienced extensive damage and die-back that have added variability to the branch diameter–length relationship, and that recovery of live branches after damage may help restore the relationship. Recovery of damaged branches may be an important mechanism for maintaining a viable branch length for supporting foliage. We identified three crown types that may be useful for characterizing the crowns of old coastal Douglas-fir. Recent studies have associated older trees with wildlife habitat and plant species diversity, and emphasized their importance in ecological management of old natural stands (Kohm and Franklin, 1997; Smith et al., 1997). Silviculturalists have shown interest in creating natural-stand-like conditions in plantations to promote more diverse management practices. Our results and observations have provided the basis for a model of crown development in old coastal Douglas-fir. Further study on the growth and development of old trees is needed in order to better understand and manage old natural stands, as well as plantation forests.

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