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A canopy perspective of community dynamics of an old-growth *Pseudotsuga-Tsuga* forest

Hiroaki Ishii

A dissertation submitted in partial fulfillment of the requirements for the
degree of

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2000

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Abstract

A canopy perspective of community dynamics of an old-growth *Pseudotsuga-Tsuga* forest

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Old-growth *Pseudotsuga-Tsuga* forests of the western Cascade Range are characterized by presence of large, old trees of *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*. Colonizing soon after a stand-replacing disturbance, *P. menziesii* is a long-lived pioneer species that persists in these forests for centuries. In this study of canopy dynamics of a 450-year-old *Pseudotsuga-Tsuga* forest, four canopy processes were found to contribute to the long-term coexistence of *P. menziesii* with late-successional species and to long-term survival of individual trees.

(1) Vertical stratification: *P. menziesii* dominates the upper-most part of the canopy, comprising nearly 70% of trees above 50m in height. Measurement and projection of current height-growth patterns indicate that this dominance will continue for at least another century.

(2) Decreasing crown competition in the upper canopy: Height growth and crown expansion culminate in large trees of all species, indicating that crown competition decreases with increasing tree size. This allows the existing large trees of different species to coexist in the upper canopy.

(3) Morphological acclimation: Old-growth *P. menziesii* have deep crowns with low branch density, and symmetric branching pattern that result in

efficient shoot and foliage display. In comparison to young and mature trees, old-growth *P. menziesii* have marked differences in crown form and branching pattern. Morphological plasticity and acclimation enable *P. menziesii* to persist into later stages of succession.

(4) Crown maintenance: Epicormic shoot production in old-growth *P. menziesii* results in adaptive reiteration of shoot cluster units, sub-branch units, and entire branches. This is an important mechanism for maintaining productivity of the established crown after height growth and crown expansion have culminated, and contributes to prolonging individual tree life-span.

Architectural characteristics generally associated with early-successional species do not apply to old-growth *P. menziesii*. Characteristics associated with persistence of *P. menziesii* may be linked with the long-term community dynamic and disturbance regime of this region. Architectural characteristics of trees change during their development, and various aspects of the species' ecology as well as its role in community dynamics need to be considered to understand the ecological significance of tree architecture.

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INTRODUCTION

Old-growth temperate coniferous forests of the Pacific Northwest Coast of North America, have some of the largest and longest-living coniferous trees in the world. Following large-scale disturbance, forest succession in the mid-elevation coniferous forests of this region generally proceeds from initial dominance by *Pseudotsuga menziesii* (Douglas-fir) to later invasion by late-successional species such as *Tsuga heterophylla*, *Thuja plicata*, *Abies amabilis*, and *Taxus brevifolia* (Hansen 1938, Munger 1940, Franklin and Hemstrom 1981). Although *P. menziesii* is considered a pioneer species, individual trees can live up to 1200 years and persist in the forest for centuries, well into later stages of succession. In their population dynamics study of a 450- to 500-year-old *Pseudotsuga-Tsuga* forest in this region, Franklin and DeBell (1988) predicted that, if current mortality rates continue, *P. menziesii* would continue to persist in the forest for an additional 755 years. Franklin et al. (1981) use the term "long-lived pioneer" to describe the persistence of *P. menziesii* into late-successional stages, and recognized the importance of large, old trees of this species in creating structural characteristics unique to the old-growth forests of this region.

Forest succession in this region is characterized by persistence of *P. menziesii* between infrequent disturbances resulting in long-term coexistence with late-successional species that may last several centuries. This community dynamic has been elucidated from population dynamics and stand reconstruction research. Recent advances in canopy access methods, such as canopy cranes and rope techniques (Lowman and Nadkarni 1996) have enabled ecologists to investigate various canopy processes that drive forest community dynamics. This research uses newly developed canopy access methods to investigate how *P. menziesii* functions as a long-lived pioneer in an old-growth *Pseudotsuga-Tsuga* forest in the Wind River Research Natural Area in southwestern Washington State, USA. In Chapter I, I investigate the vertical development of the forest canopy to understand current patterns of vertical stratification among species, the role of *P. menziesii* as a dominant species in the upper canopy, and to predict future dynamics of the forest canopy. In Chapter II, I compare architectural characteristics and growth of coexisting canopy tree species and discusses the role of architectural variation and crown competition in contributing to long-term species coexistence. In Chapter III, I elucidate the mechanism by which foliage is maintained in the established crown of *P. menziesii* trees through continuous production of epicormic shoots. In the concluding chapter, I synthesize the findings and present a dynamic theory on the ecological significance of tree architecture that takes into account long-term community dynamics of old-growth *Pseudotsuga-Tsuga* forests.

CHAPTER I

Height growth and vertical development of an old-growth *Pseudotsuga-Tsuga* forest in southwestern Washington State, U.S.A.

Introduction

Vertical stratification among tree species has been found in various forest types including tropical rain forests (Richards 1952, Grubb et al. 1963, Ashton and Hall 1992), temperate broad-leaved forests (Kira et al. 1969, Sumida 1995), and temperate coniferous forests (Ogino 1990, Easter and Spies 1994). Vertical partitioning of the forest canopy among tree species has been suggested as a factor promoting species coexistence (Cody 1986, Kohyama 1993). Vertical stratification is defined by both the regeneration ecology of species and their height-growth patterns (Johnson et al. 1994, Dubrasich et al. 1997). Regeneration ecology reflects the relative shade tolerance of species and determines whether individuals are found in the understory. It has been investigated in detail in studies on forest succession, e.g., Stewart (1986), Franklin and DeBell (1988), and Gray (1996), in the Pacific Northwest U.S.A. Height-growth patterns determine the height distributions of species, and are defined by their height-growth rate and maximum attainable height. Several studies have reconstructed the recruitment, survival and height-growth patterns of mixed-species forests to infer the development of vertical stratification (Oliver and Stephens 1977, Wierman and Oliver 1979, Bicknell 1982, Kelty 1986, Palik and Pregitzer 1993).

Silvicultural studies have estimated height-growth patterns of tree species from empirically derived site-index curves differing by site quality (Miyajima 1989, Hann 1995). A similar approach to inferring height-growth patterns of species has been applied to mixed-species natural stands by substituting tree diameter for tree age and deriving static diameter-height relationships of existing trees (Fujimori et al. 1976, Aiba and Kohyama 1996, Thomas 1996). Height-growth patterns inferred from static diameter-height relationships have been used to interpret current patterns of vertical stratification among species and to infer future forest dynamics. Thomas (1996) compared static diameter-height relationships among species in a Malaysian rain forest in relation to their life histories and onset of reproduction. Aiba and Kohyama (1996) used static diameter-height relationships to derive "projected maximum size" of tree species in a warm-temperate rain forest in southern Japan, and compared these values in relation to tree demography.

Using diameter as a surrogate for tree age and interpreting the static diameter-height relationship as the dynamic height-growth pattern of a species requires assuming that changing growth conditions through time at a given site does not alter the diameter-height relationship (Thomas 1996). However, as tree form and allometry are influenced by both environmental and competitive factors (Holbrook and Putz 1989, King 1991), temporal changes in these conditions are likely to affect the diameter-height relationship. In mixed-species natural stands, species differences in relative shade-tolerance and successional status will result in differences, over time, in the abundance and range of tree sizes observed for each species. This may cause varied uncertainty among species in estimating diameter-height relationships at any given time. Variation and uncertainty resulting from temporal changes must be considered when interpreting static diameter-height relationships of mixed-species natural stands.

In addition, the effects of environmental and competitive factors on the diameter-height relationship must also be considered. The effects of environmental conditions and competitive interaction on height growth and diameter-height relationships are well documented (e.g. Ritchie and Hann 1986, Hann and Ritchie 1988, Krumland and Wensel 1988). Damaging agents such as wind, snow, herbivory, pathogens, and falling debris and litter have negative impacts on height growth (Shidei 1976, Putz et al. 1983, Clark and Clark 1991, Telewski 1995, Tainter and Baker 1996). Some forms of competitive interaction, such as shading from above, have also been found to result in reduction of resources and suppression of height growth (Kohyama 1980, O'Connell and Kelty 1994, King 1997). The effects of and response to environmental conditions and competitive interactions may vary depending on the species.

Information on current growth rates is also useful for inferring future dynamics of height growth. There is general agreement that height-growth rates decrease as trees near their maximum attainable height (Assman 1970, Hallé et al. 1978, Ogino 1990). However, as Stevens and Perkins (1992) and Ryan and Yoder (1997) have noted, the underlying ecological and physiological mechanisms determining height-growth patterns are still to be investigated. A detailed analysis of diameter-height relationships coupled with current growth rates will help to elucidate patterns of tree height growth and to predict future dynamics of mixed-species natural stands.

This study explores the variability found in the diameter-height relationships of species in an old-growth *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* (Douglas-fir)- *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) forest in southwestern Washington State, U.S.A. The varying effects of damage and shading on the diameter-height relationships are investigated. In addition, current height-growth rates are estimated from measurements of terminal shoot elongation rates. These observations are combined to predict the future development of vertical stratification in this forest.

Study site and methods

The study was conducted in an old-growth *P. menziesii* - *T. heterophylla* forest at the Wind River Canopy Crane Research Facility located in the Thornton T. Munger Research Natural Area, Gifford Pinchot National Forest in southwestern Washington State, U.S.A. (45°49'N, 121°57'W; altitude 355m). The stand is dominated by *P. menziesii* and *T. heterophylla* in terms of basal area. *Thuja plicata* Donn ex D. Don (western red cedar), *Abies amabilis* Dougl. ex Forbes (Pacific silver fir) and *Taxus brevifolia* Nutt. (Pacific yew) are also abundant. Other tree species in the stand include: *A. grandis* (Dougl. ex D. Don) Lindl. (grand fir), *Pinus monticola* Dougl. ex D. Don (western white pine), and *Cornus nuttalii* Audubon (Pacific dogwood). Franklin (1972) and Franklin and DeBell (1988) give a detailed description of the area.

Four hectares of old-growth forest (400 to 500 years old) were mapped, and diameter at breast height (DBH) and height of all trees > 5 cm DBH were measured. DBH was measured with a diameter tape 1.3 m above ground level, except for trees with multiple stems below 1.3 m, in which case it was measured below the point where the stems parted. Tree height was defined as the vertical distance from ground level to the highest foliage on the tree. Heights of trees shorter than ca 10 m were measured with a 15 m telescoping height pole, while heights of taller trees were calculated by the Laser Impulse Rangefinder (Laser Technology Inc.) using angle-distance measurements.

The main stem of each tree was examined for evidence of past damage, using binoculars and the Wind River Canopy Crane (Parker 1997) for tall trees. Damage was divided into five categories: (1) leaning of the main stem >15 degrees from the vertical; (2) forks and crooks in the main stem that reflect past breakage and resprouting; (3) broken tops reflecting recent loss of the leader; (4) top die-back or loss of foliage at the top of the tree; and (5) other damage which included infection of the leader by dwarf mistletoe (observed in *T. heterophylla*), and significant branch loss due to abrasion from an adjacent tree fall. The categories are in order of dominant damage effects; a tree whose main stem leans and also forks was classified under category (1).

Trees growing under the closed canopy were examined for evidence of vertical suppression due to shading. A tree was considered suppressed when the terminal shoot could not be clearly distinguished (observed in *T. plicata* and *T. heterophylla*) or had stunted growth and was lower in height than the lateral shoots (observed in *A. amabilis* and *T. brevifolia*). If a tree was both damaged and suppressed it was classified as damaged. Trees without evidence of damage or suppression were classified as "intact."

Variability of diameter-height relationships

The exponential generalization of the allometric equation (Arabatzis and Burkhart 1992, Thomas 1996),

[1] $H = H_{\max} \{ 1\text{-}\exp (- aD^{b}) \}$,

was fit to all trees of the five most abundant species (in order of abundance: *T. heterophylla, T. brevifolia, A. amabilis, P. menziesii,* and *T. plicata*). a, b and $H_{\max}$ are nonnegative parameters estimated using the bounded nonlinear least squares regression function, *nlregb,* in S-Plus 4.5 (MathSoft). $H_{\max}$ is the model estimate of maximum attainable height for the species. While this fitting procedure does not account for measurement error in the diameter observations, it does allow direct fitting of the nonlinear equation.

Uncertainty in the parameter estimates must be considered when comparing estimates among species. Therefore, 90 and 95% confidence intervals were calculated for each estimate of $H_{\max}$. For each regression, the statistical assumptions required for use of parametric confidence interval estimation, namely constant variance and normality of residuals, were visually investigated. Nonconstant residual variance can result in biased standard error estimates, and hence biased confidence intervals. If these assumptions were violated, bias-corrected and accelerated (Bca) bootstrap confidence intervals were calculated using 1000 bootstrap replicates (Huet et al. 1990), following the procedure in Lunneborg (1999).

Effects of damage and shading

The above procedure was repeated using only the intact trees of each species to examine the effects of damage and shading on the diameter-height relationship and on estimates of $H_{\max}$ and its uncertainty. In addition, the frequency of damaged and suppressed trees was calculated for each species by height class to determine if these effects were random or size-dependent. The relative distributions of each species' damaged and suppressed trees were compared with that of the intact trees using the Kolmogorov-Smirnov two-sample test (K-S test, Conover 1980). If the effects are random, then the height distributions of damaged and suppressed trees should not differ from that of the intact trees.

Current height-growth rates

Terminal shoot elongation rates were measured for intact, non-suppressed trees of the four canopy-level species (22 *P. menziesii*, 44 *T. heterophylla*, 17 *T. plicata*, and 9 *A. amabilis*), assuming that healthy, non-suppressed trees of various sizes would represent the current maximum height-growth rates of the species in the stand. Trees were chosen that had a clearly distinguishable terminal shoot, had no evidence of damage or suppression to the main stem, and were not growing under any other tree. The terminal shoot of each tree was visited using the Wind River Canopy Crane at the end of the 1997 growing season. For *P. menziesii*, *T. heterophylla* and *A. amabilis*, distances between bud scars on the terminal shoot were measured for the past three years of growth (1995-1997) and averaged to obtain mean terminal shoot elongation rate per year. *T. plicata* produces no distinguishable bud scars, and determining past terminal shoot elongation can be difficult and possibly inaccurate (Parker and Johnson 1987). Therefore, terminal shoot elongation for the following year (1998) was measured by marking the base of the terminal shoot at the end of the 1997 growing season, and returning at the end of the following season to measure the increase in the distance from the mark to the tip of the terminal shoot.

Results

The relative abundance of the five most abundant species by 5 m height classes showed evidence of vertical stratification among species (Figure 1.1). *P. menziesii* dominated in height classes above 50 m but was completely absent in height classes below 30 m. No regeneration of *P. menziesii* was observed in the stand. *T. heterophylla* dominated in height classes from 10 to 45 m, *T. plicata* was found throughout all height classes, *A. amabilis* was found mainly in height classes below 45 m, and *T. brevifolia* was found only in height classes below 20 m.

Variability of diameter-height relationships

Equation [1] was well fit to the diameter-height relationship of all trees of *T. plicata*, *T. heterophylla* and *A. amabilis* ($r^2 > 0.90$; Figure 1.2, all trees). However, the model failed to explain a large proportion of the height variation in *P. menziesii* and *T. brevifolia* ($r^2 = 0.524$ and 0.500, respectively), both of which were observed over a relatively limited range of sizes compared to other species.

Residuals from the model fits tended to display increasing variance with both increasing diameter and with increasing predicted height. This biases the standard error estimates used in parametric confidence interval calculations. Therefore, bootstrap confidence intervals were calculated for each species' H_{max} estimates. Both the 90% and 95% confidence intervals were calculated to reveal the possible skewness present in each species' bootstrap distributions of H_{max} estimates (Figure 1.3; all trees).

The uncertainty of the estimates varied widely. The greatest uncertainty was observed in *T. brevifolia*. Given the uncertainty associated with each estimate, only the H_{max} estimate of *A. amabilis* could be distinguished as being lower than those of {*P. menziesii*, *T. heterophylla*, and *T. plicata*}.

Effects of damage and shading

Refitting equation [1] to the diameter-height relationship for only the intact trees of each species improved the fit (increased r^2) for all species, and consistently increased the predicted height for a given diameter (Figure 1.2; intact only). Species differed, however, as to the trend in differences in predicted heights between the two regressions, suggesting that damage and shading have variable effects on predicted height estimates depending on the species and on tree size (Figure 1.4). *T. plicata*, *A. amabilis*, and *T. brevifolia* all showed increasing differences in predicted heights with increasing diameter, though *A. amabilis* showed very small differences below 20 cm in diameter.

While *T. heterophylla* showed initially increasing differences in predicted heights with increasing diameter, the difference peaked around 60 cm in diameter and declined thereafter. Alternatively, *P. menziesii* showed decreasing difference between predicted heights with increasing diameter. The greatest maximum differences in predicted heights between the two regressions were observed for *T. plicata* and *T. brevifolia* (5.78 m and 3.99 m, respectively).

Estimates of $H_{\max}$ also consistently increased after excluding damaged and suppressed trees (Figure 1.3: intact only). The increases were considerable for *T. plicata* and *T. brevifolia* (9.5 m and 36.8 m, respectively), and relatively small for the other species. Except for *T. heterophylla*, the uncertainty associated with each species' $H_{\max}$ estimate increased. This partly resulted from the decreased sample sizes used. As a result, only the $H_{\max}$ estimate of *A. amabilis* could be distinguished as being lower than those of {*P. menziesii*, and *T. plicata*}, and the estimate of *T. heterophylla* as being lower than that of *T. plicata*. The unrealistically large value and large uncertainty in the $H_{\max}$ estimate for *T. brevifolia* resulted from the fact that observations were limited to the smaller tree sizes, providing little information for estimating the model asymptote.

Main causes of damage and relative distribution of damage by height class differed among species (Figure 1.5). For *P. menziesii*, resprouted/forked main stem and top die-back were the main causes of damage, over 85% of trees in the 30-40 m height class showed evidence of past breakage, and damage in general increased with decreasing height class (K-S test, $P < 0.01$). For *T. heterophylla*, resprouted/forked main stem was the main cause of damage, and the relative height distribution of damaged trees could not be distinguished from that of the intact trees (K-S test, $P = 0.19$), suggesting that damage was not size-dependent in this species. For *T. plicata*, resprouted/forked main stem and top die-back were the main causes of damage, over 35% of trees in the tallest height class (50-60 m) showed top-die back, but damage in general was not size-dependent in this species (K-S test, $P = 0.58$). For *A. amabilis*, resprouted/forked main stem and top die-back were the main causes of damage, and damage in general increased with increasing height class (K-S test, $P = 0.06$). For *T. brevifolia*, leaning and resprouted/forked main stem were the main causes of damage. Leaning was more common in height classes below 4 m while resprouted/forked main stem was more common in the 4 to 12 m height classes, and damage in general increased with decreasing height class (K-S test, $P = 0.01$). Suppression due to shading increased with decreasing height class in all species (K-S test, $P < 0.01$ for all species), suggesting, not unexpectedly, that the effects of shading on tree height was skewed toward shorter trees.

Current height-growth rates

Terminal shoot elongation rates of intact, non-suppressed trees displayed a decreasing trend with increasing tree height for *P. menziesii* and *T. plicata* (Figure 1.6, $r = -0.50$, $P = 0.02$, and $r = -0.52$, $P = 0.03$, respectively). Terminal shoot elongation rates ranged from 2.9 to 10.6 cm•year^{-1} for *P. menziesii*, and 3.9 to 34.0 cm•year^{-1} for *T. plicata*. Terminal shoot elongation rates showed an increasing and then decreasing trend with increasing tree height for *T. heterophylla*. Minimum terminal shoot elongation rate for this species was

4.2 cm•year^{-1}, and maximum terminal shoot elongation rate was 34.7 cm•year^{-1} observed around 30 m in tree height. No clear trend in terminal shoot elongation rates was found in *A. amabilis.*

For both *P. menziesii* and *T. heterophylla*, terminal shoot elongation rates reached minimum values near the $H_{\max}$ estimated from the diameter-height relationship of intact trees. While the tallest trees of *T. plicata* were still more than 10 m shorter than the estimated $H_{\max}$ of 68.5 m, and their terminal shoot elongation rates were more variable. The wide range of terminal shoot elongation rates observed above 40 m in height for *T. plicata* may be due to annual variation, as measurements were only made for one year's growth in this species.

Discussion

The amount of variation around the diameter-height regression and the degree of uncertainty in the $H_{\max}$ estimates reflected differences among species in their relative abundance and size structure. The greatest variation and uncertainty were found for *P. menziesii*, a shade-intolerant, early successional species, whose size range was limited to large trees, and for *T. brevifolia*, an extremely shade-tolerant, late successional species, whose size range was limited to small trees. Other species showed less variation and uncertainty as a result of their high abundance and wide range of tree sizes. Note that while limited observation ranges need not translate into larger uncertainties in linear regression, it can have extreme impact in fitting nonlinear models (Draper and Smith 1981).

Species differences in variation and uncertainty associated with the diameter-height relationship reflected well the transitional succession stage of this stand. Differences among species in their relative abundance and size structure are characteristic of forests in transitional stages of succession (Stewart 1986b). As a consequence of the long life-spans of trees, species succession in the coniferous forests of the Pacific Northwest proceeds at a much slower rate than in other forest types where more rapid, seral replacement of species is observed (Spies et al. 1990). Sprugel (1991) pointed out that old-growth forests in this region are still at a transition stage in succession and have been so for centuries. It is likely that species composition and structure of the forest has changed over time and will continue to do so for the next several hundred years (DeBell and Franklin 1987, Franklin and DeBell 1988). Constant changes in growth conditions result in changes in species composition and differential development of individual trees, making it difficult to interpret diameter as a surrogate for tree age (Stewart 1986b). It is likely that the variation and uncertainty associated with diameter-height relationships of the species in this stand will continue to change over time, and that such changes will have an affect on our ability to infer height-growth patterns from static diameter-height relationships.

Excluding damaged and suppressed trees from the static diameter-height relationship consistently increased predicted heights and $H_{\max}$ estimates in all species. In addition, uncertainties around the $H_{\max}$ estimates increased in all but one species. The largest increase in both predicted height and $H_{\max}$ estimates were observed in *T. plicata* and *T. brevifolia*. The negative impact of environmental factors such as wind and snow damage leading to stem breakage and die-back have been reported for various forest types (Goto and Nitta 1990, Everham III 1995, Nykanen et al. 1997). Shaded trees have been shown to have reduced growth in comparison to open-grown trees of the same species (Kohyama 1980, O'Connell and Kelty 1994). Of the total number of trees in this study, 44.1% showed evidence of damage or suppression of terminal shoot growth. The growth of individual trees in Pacific Northwest forests is affected continuously by environmental and competitive factors over their long life-span, resulting in widely varied growth patterns among individual trees and across species (Edmonds et al. 1992). The effects of damage and shading on predicted height estimates were variable depending on the species and on tree size. Predominant damaging agents and size dependency of damage also differed among species. These results emphasized the importance of considering differential effects of various damaging agents and competitive interactions in studies of height-growth pattern.

Measurements of terminal shoot elongation rates revealed trends in current height-growth rates with tree height for *P. menziesii*, *T. heterophylla* and *T. plicata*. Maximum terminal shoot elongation rate in *P. menziesii* was about one-third that of *T. heterophylla* and *T. plicata*, and considerably lower than maximum height-growth rates reported by Ritchie and Hann (1986) for younger *P. menziesii* (18-137 years old, growth rates ranging from 67 cm•year^{-1} to 110 cm•year^{-1}). Values for minimum terminal shoot elongation rate were more constant across species. The decline in terminal shoot elongation rate with increasing height found for *P. menziesii* and *T. plicata*, and for *T. heterophylla* above 30 m in height, may lead to reduced apical control and result in "multiple tops" or "flat tops," characteristic of trees that are said to be near their maximum attainable height (Brown et al. 1967). Many of the intact, non-suppressed trees of *T. heterophylla* below 20 m in height were growing in gaps. Their low height-growth rates may be the result low light conditions at the bottom of gaps. Coniferous forests have low gap-size ratios (deep, narrow gaps) and low incident angles of sun light, resulting in low light environments at the bottom of gaps (Canham et al. 1990, Spies et al. 1990, Easter and Spies 1994). Increased crown closure and low incident light have been shown to result in reduced rates of height growth (Ritchie and Hann 1986, Hann and Ritchie 1988). For short trees growing in gaps, height-growth rate is likely to increase as tree height increases, as a result of the positive feedback between improved light conditions and accumulation of foliage area. The changes in height-growth rate with tree height observed for *T. heterophylla* may also characterize other shade tolerant species in this stand, such as *A. amabilis*. Additional information on the three-dimensional position of these trees in the stand may provide a more accurate explanation of the height-growth patterns observed (Ritchie and Hann 1986, Hann and Ritchie 1988).

The results of the diameter-height relationships, effects of damage and shading and current height-growth rates were combined to infer future development of the forest canopy. High incidence of damage in height classes below 50 m and declining height-growth rates with increasing tree height suggested that the *P. menziesii* population as a whole may be near their maximum attainable height. The *T. heterophylla* population had abundant understory trees that have the potential for further height growth as damage was not size dependent in this species. Current height-growth rates for *T. heterophylla* also suggested that trees ranging in height from 20 to 35 m have the potential to grow considerably in height. As a result, the *T. heterophylla* population as a whole has the potential to increase in height. The *T. plicata* population also had several understory trees that have the potential for further height growth as damage was also not size dependent in this species. Although terminal shoot elongation rates for *T. plicata* showed a declining trend with increasing tree height, most trees were still far from the predicted maximum attainable height and some tall trees showed relatively high height-growth rates. The *A. amabilis* population also had abundant understory trees. However, the maximum attainable height estimate for this species was more than 10 m shorter than the other canopy level species. In addition, damage increased with increasing height class suggesting that damage may also be a factor limiting the maximum attainable height of the population. *T. brevifolia* is empirically known as an understory to lower canopy species with adult heights in this region usually ranging from 7 to 15 m (King 1991) with maximum height around 25 m (Sudworth 1967, Arno and Hammerly 1977). Height growth of understory trees of this species may also be limited, as damage increased with decreasing height class.

These results suggest that the future development of the forest canopy would involve a slow invasion of the upper canopy by *T. heterophylla* and *T. plicata*, while *A. amabilis* and *T. brevifolia* continue to survive in the lower canopy. However, at current height-growth rates of 4 to 5 cm•year^{-1} for the tallest trees of *T. heterophylla*, it would take them nearly 100 years to reach heights comparable to the dominant trees of *P. menziesii*. Although some of the tallest trees of *T. plicata* showed relatively high height-growth rates, this species had low relative abundance in the upper canopy. In their population dynamics study of the same area, Franklin and DeBell (1988) predicted that, if current mortality rates continue, *P. menziesii* would continue to persist in this forest for 755 more years. Given their long life-span of nearly 1200 years (Franklin et al. 1981), it is likely that *P. menziesii* will continue to maintain its dominant status in the upper canopy for at least another century.

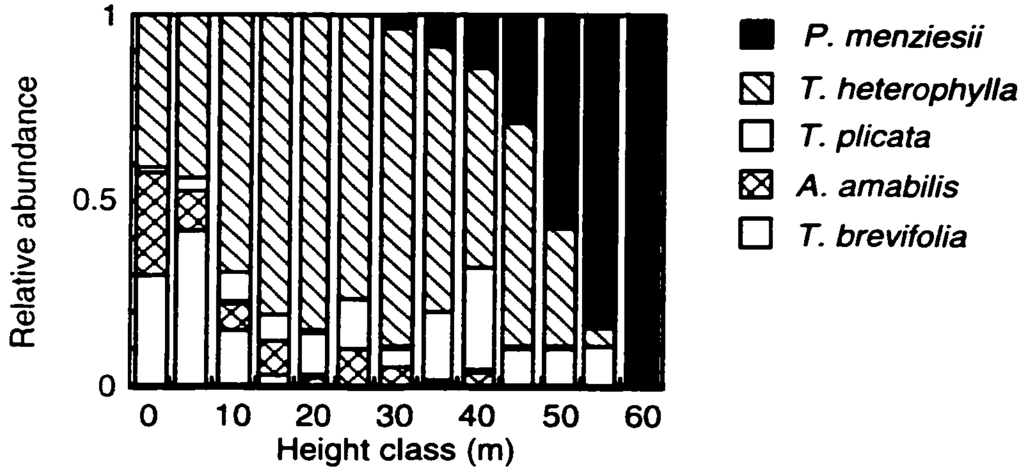


Figure 1.1. Relative abundance of the five most abundant tree species by height class showing vertical stratification of species.

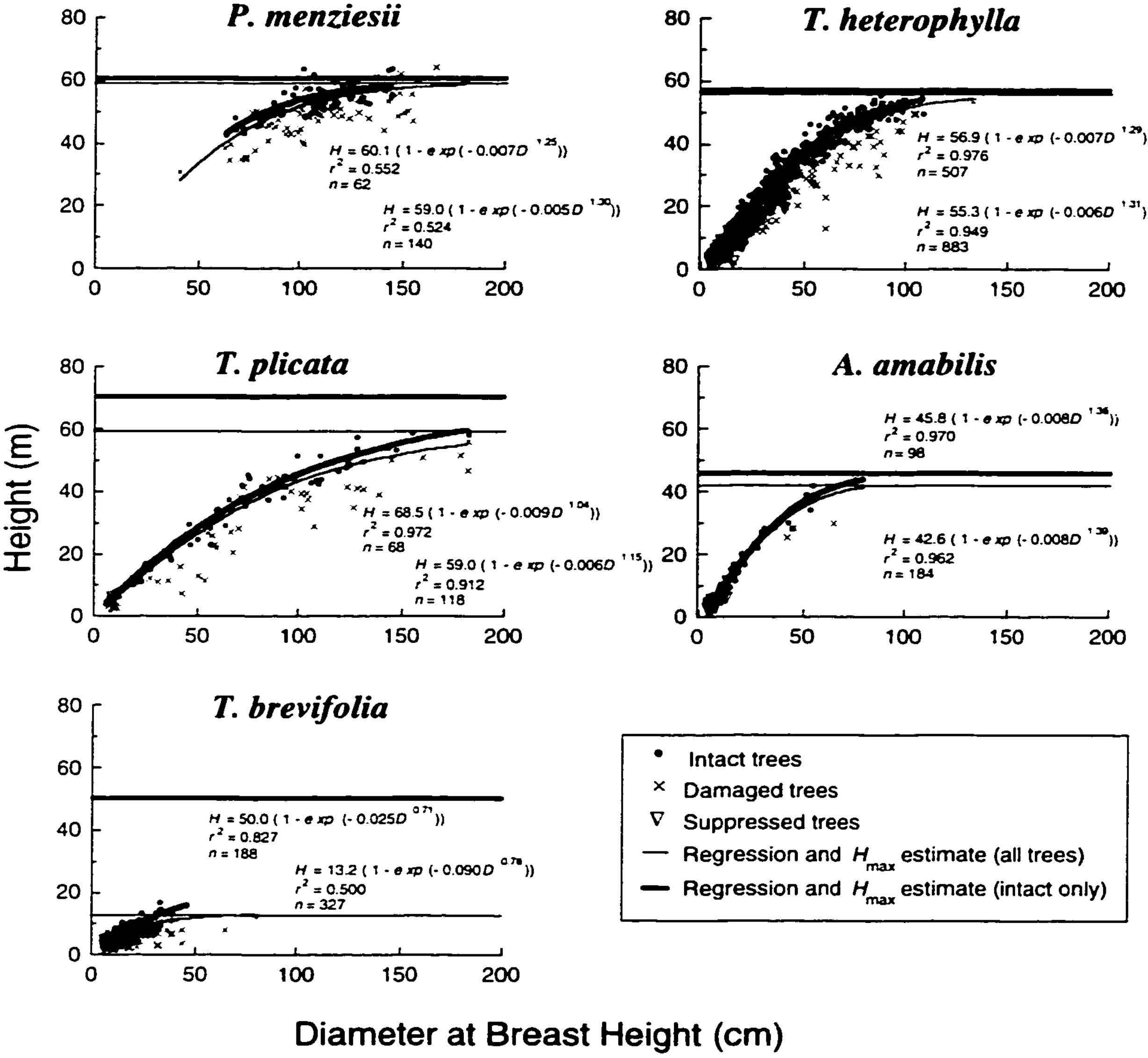


Figure 1.2. Diameter - height relationships of the five most abundant tree species. Non-linear least-squares regression fits of Equation [1] and *Hmax* estimates are shown for all trees > 5 cm DBH (thin lines) and for intact trees (•) only (thick line). Damaged (x) and suppressed (∇) trees were excluded from the latter regression analysis.

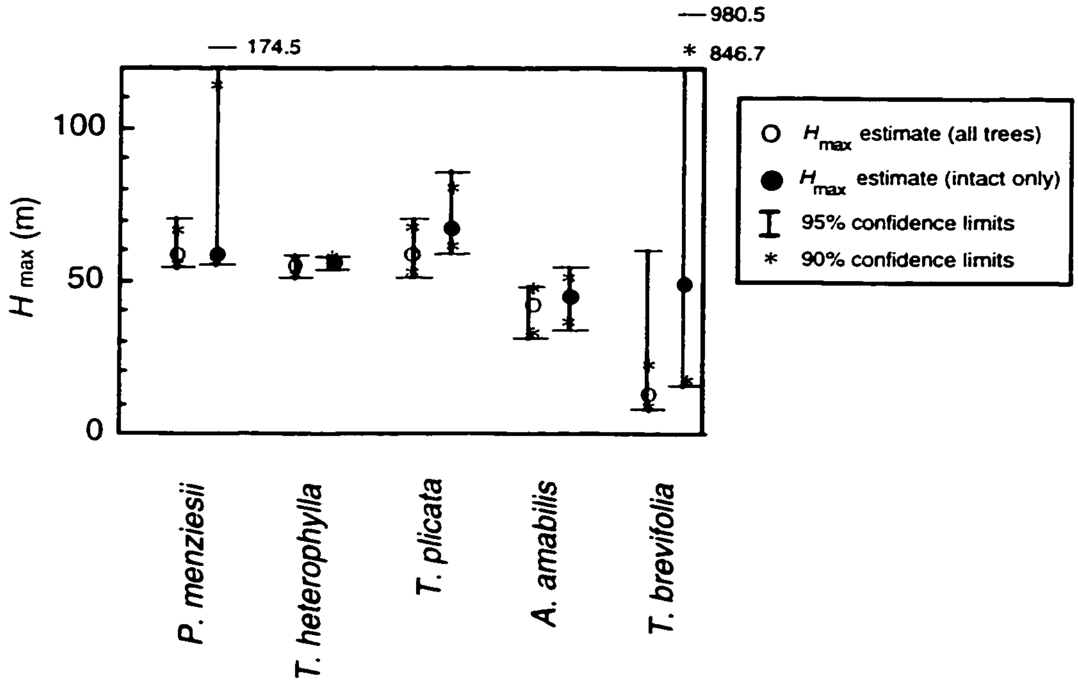


Figure 1.3. Estimated $H_{\max}$ for all trees > 5 cm DBH (open circles) and for intact trees only (solid circles) with 90% (*) and 95% (—) bootstrap confidence limits.

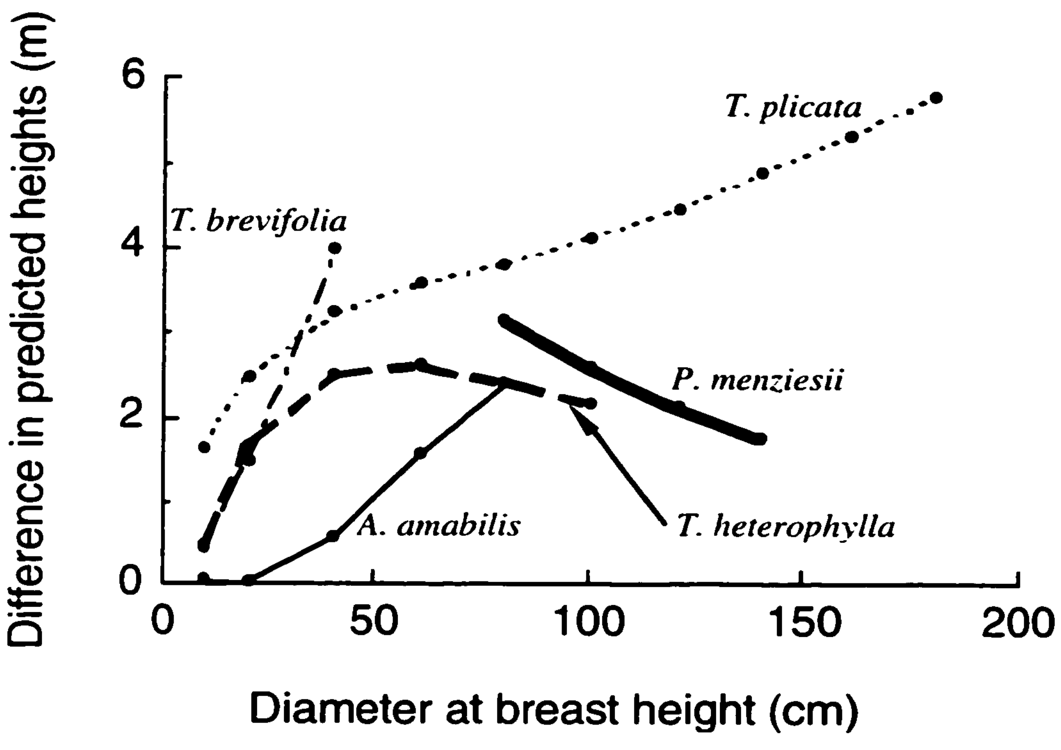


Figure 1.4 The difference in predicted heights between the regression using all trees and the regression using intact trees only. Predicted heights were calculated at 20 cm intervals within the range of DBHs observed for each species.

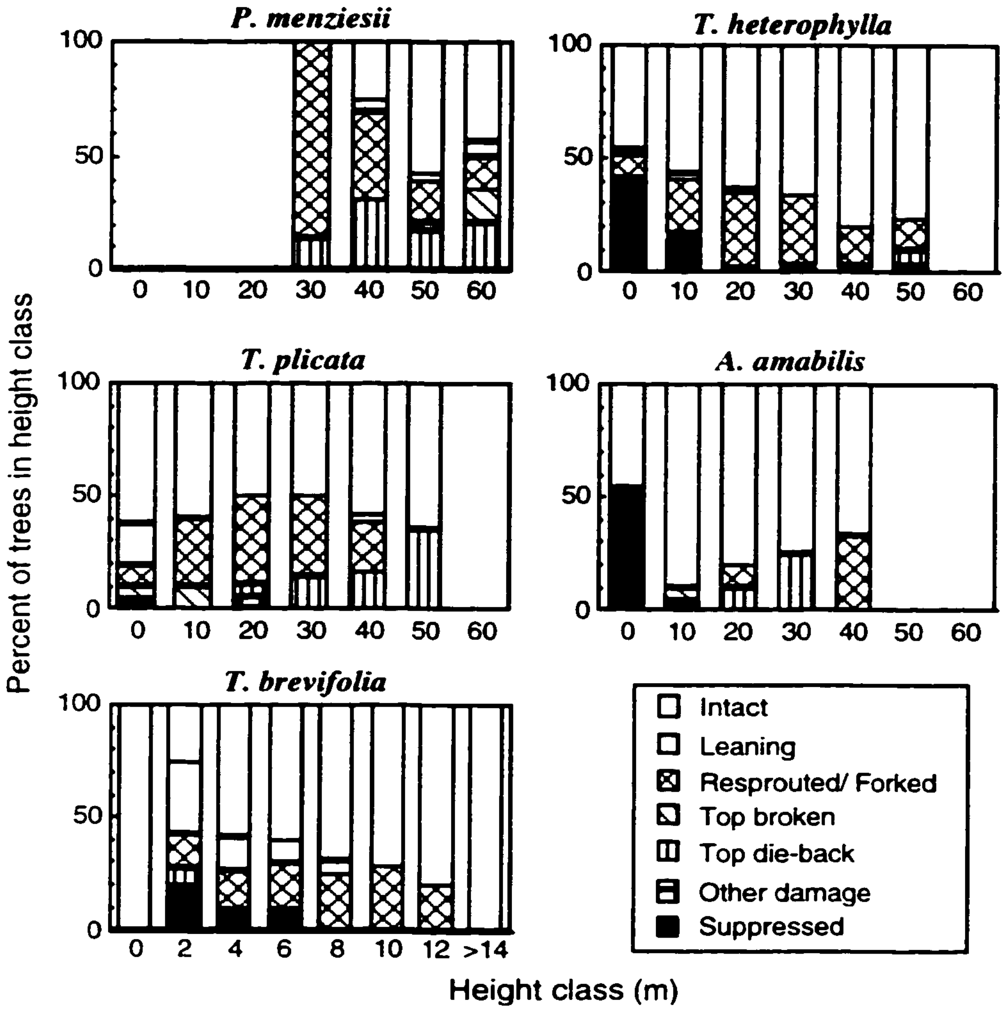


Figure 1.5. Relative frequency distributions by height class for each species' intact (open bars), damaged (hashed bars) and suppressed (solid bars) trees. Note different height classes for *T. brevifolia*.

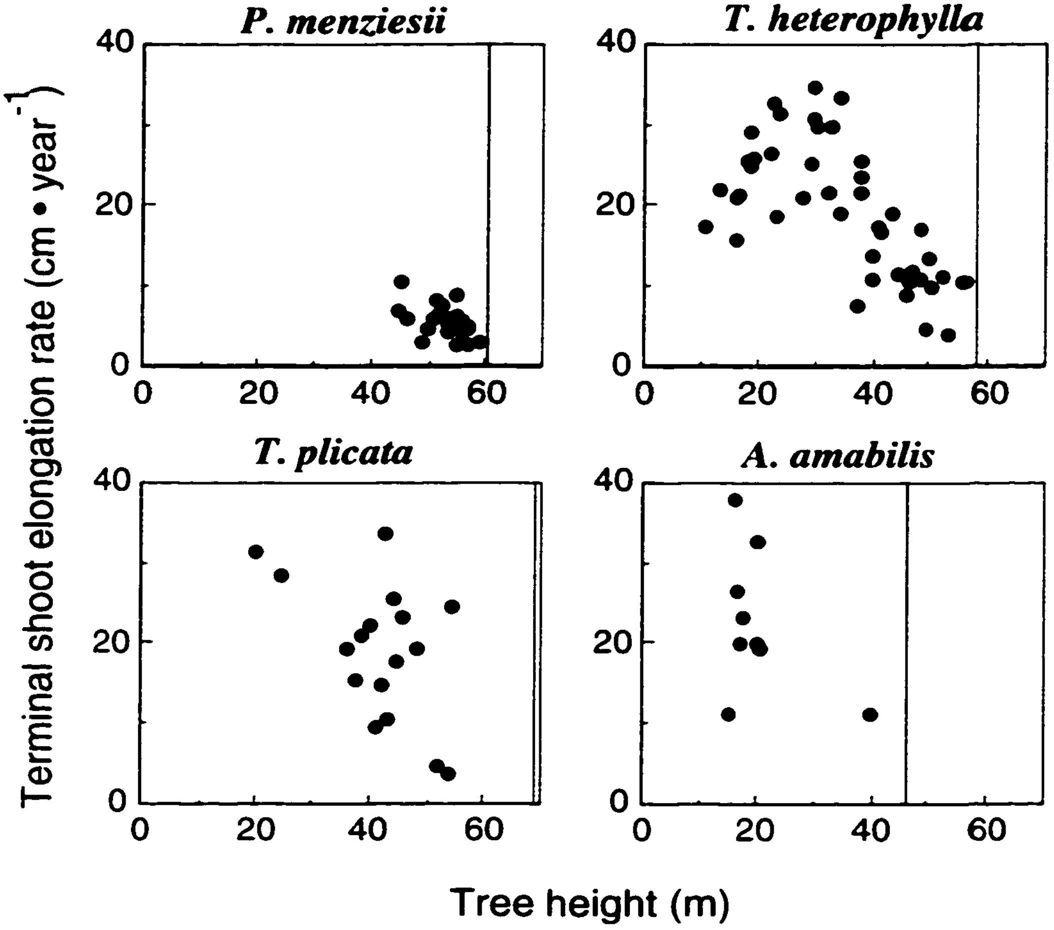


Figure 1.6. The relationship between tree height and terminal shoot elongation of intact, non-suppressed trees. Vertical lines indicate H_{max} estimates from diameter-height relationships of intact trees.

CHAPTER II

A canopy perspective of long-term species coexistence in an old-growth *Pseudotsuga-Tsuga* forest

Introduction

Old-growth temperate forests of the Pacific Northwest Coast of North America have some of the largest and longest-living coniferous trees in the world (Waring and Franklin 1979). Following large-scale disturbance, forest succession in mid-elevation coniferous forests of this region generally proceeds from initial dominance by *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* (coastal Douglas-fir) to later invasion by late-successional species such as *Tsuga heterophylla* (Raf.) Sarg. (western hemlock), *Thuja plicata* Donn ex D. Don (western red cedar), *Abies amabilis* Dougl. ex Forbes (Pacific silver fir), and *Taxus brevifolia* Nutt. (Pacific yew) (Munger 1940, Franklin and Hemstrom 1981, Spies and Franklin 1989, Stewart 1989). Although *P. menziesii* is considered a pioneer species, individual trees can live over 1000 years and persist in the forest for centuries, resulting in long-term coexistence of *P. menziesii* with late-successional species (Franklin and DeBell 1988).

Ishii et al. (2000) found vertical stratification among canopy tree species in a 450-year-old *Pseudotsuga-Tsuga* forest in southwestern Washington State, USA, and showed that *P. menziesii* dominates in the upper canopy, comprising 68% of trees above 50m in height, while shade-tolerant, late-successional species such as *T. heterophylla*, *T. plicata*, *A. amabilis*, and *T. brevifolia* dominate in the mid to lower canopy. Through analyses and projection of height-growth rates, they found no differences in maximum attainable height among *P. menziesii*, *T. heterophylla*, and *T. plicata*. *A. amabilis* was distinguished as having lower maximum attainable height, restricting it to the mid to lower-canopy. Although maximum attainable height for *T. brevifolia* could not be accurately determined due to very large uncertainty, empirical evidence suggests that it is restricted to the lower canopy. Ishii et al. (2000) predict that *P. menziesii* will remain dominant in the upper canopy of this forest for at least another century, while *T. heterophylla* and *T. plicata* slowly invade the upper canopy, and *A. amabilis* and *T. brevifolia* are restricted to the mid to lower canopy.

P. menziesii is known to dominate in the upper canopy during early stages of succession in mixed-species second-growth forests of this region (Wierman and Oliver 1979, Larson 1986). Studies of canopy structure in old-growth forests have found that *P. menziesii* continue to survive in the upper canopy for up to 800 years (Gholz et al. 1976, Stewart 1986a, Stewart 1986b, Spies et al. 1990, Easter and Spies 1994). In their population dynamics study of the same old-growth stand as Ishii et. al (2000) and this study, Franklin and DeBell (1988) predict that, if current mortality rates continue, *P. menziesii* would persist in the forest for an additional 755 years. These observations suggest that dominance of *P. menziesii* in the upper canopy of old-growth *Pseudotsuga-Tsuga* forests is largely the result of differences among species in their timing of establishment, and can last for centuries. Prolonged dominance of relatively shade-intolerant *P. menziesii* in the upper canopy, above the more shade-tolerant, late-successional species, may contribute to their long-term coexistence.

Another canopy process contributing to long-term coexistence of *P. menziesii* with late-successional species may be decreasing competition among large trees in the upper canopy. Competition among species for a single resource, such as light, often results in exclusion of species (Tilman 1988). However, competing species can coexist if resource availability oscillates, or is spatially variable, and the effects of competition are localized (Shmida and Ellner 1984, Tilman 1988). In a study of the horizontal spatial distribution of trees in the same old-growth stand as Ishii et al. (2000) and this study, Freeman (1997) found that trees with diameter at breast height < 20 cm are spatially aggregated by species, while trees ≥ 20 cm are evenly distributed across all species. Moeur (1993) found similar results for a *T. heterophylla* forest in northern Idaho, and presented a conceptual model of tree competition in which intense competition among small trees results in even spatial distribution and decreasing competition as trees increase in size (Moeur 1997). Decreasing competition with increasing tree size may allow large trees of different species that survive the initial competitive exclusion stage to coexist in the upper canopy of forests. Both Moeur (1993) and Freeman (1997) inferred patterns of competition from spatial distribution. However, above-ground competition for light is the direct result of interactions between tree crowns (crown competition), and measurements of crown growth would provide more direct inferences regarding above-ground competition.

A high degree of morphological plasticity may also contribute to long-term survival of *P. menziesii* by allowing this species to acclimate to changing stand conditions as succession proceeds and late-successional species invade the stand. Canham (1988) found high degrees of morphological plasticity in branching pattern and foliage display in *Acer saccharum* Marsh. (sugar maple), and proposes that morphological acclimation may be more readily achieved than physiological acclimation because it involves less metabolic costs. Crown form of old-growth *P. menziesii* is markedly different from that of young trees (Franklin et al. 1981), and this implies high degrees of morphological plasticity in this species. At a smaller morphological scale, I observed that branching pattern of old-growth *P. menziesii* is markedly different from that of young trees, and similar to two coexisting late-successional species, *A. amabilis* and *A. grandis* (Dougl. ex D. Don) Lindl. (grand fir).

Recent advances in canopy access techniques (Lowman and Nadkarni 1996) enable direct investigation of canopy processes that drive forest community dynamics. In this study, I used the Wind River Canopy Crane to make direct, non-destructive, and repeated measurements of the live crown of large canopy trees. I investigated three canopy processes that may contribute to long-term coexistence of *P. menziesii* with late successional species in old-growth *Pseudotsuga-Tsuga* forests: (1) vertical stratification, (2) crown competition, and (3) morphological acclimation. Vertical distribution of live crowns, horizontal crown expansion rates, and variation among species in crown form and branching pattern, are compared among four coexisting canopy tree species: *P. menziesii*, a long-lived pioneer, and three late-successional species, *A. amabilis, A. grandis*, and *T. heterophylla*, in a 450-year-old *Pseudotsuga-Tsuga* forest in southwestern Washington State, USA. Vertical distribution of live crowns are compared to elucidate patterns of vertical stratification among species. Horizontal crown expansion rates are compared in relation to the light environment to infer intensity of crown competition for light. Crown form and branching pattern are compared to infer species differences in strategies for shoot and foliage display. I then discuss how, together, these three canopy processes contribute to long-term coexistence of *P. menziesii* with late-successional species, and how *P. menziesii* functions as a long-lived pioneer in old-growth *Pseudotsuga-Tsuga* forests.

Study site and Methods

The study was conducted in an old-growth *P. menziesii - T. heterophylla* forest at the Wind River Canopy Crane Research Facility located in the Thornton T. Munger Research Natural Area, Gifford Pinchot National Forest in southwestern Washington State, USA (45°49'N, 121°57'W; altitude 355m). Stand basal area is dominated by *P. menziesii* and *T. heterophylla*. Species such as *T. plicata*, *A. amabilis* and *T. brevifolia* are also abundant. Other tree species in the stand include: *A. grandis*, *Pinus monticola* Dougl. ex D. Don (western white pine), and *Cornus nuttalii* Audubon (Pacific dogwood). Franklin (1972) and Franklin and DeBell (1988) give a detailed description of the area.

The Wind River Canopy Crane is a free-standing construction tower crane enabling in-situ study and measurement of canopy-level trees within a 2.27 ha circular area of old-growth forest. Because the facility is a collaborative research area, destructive sampling is restricted in order to maintain site integrity for future ecological study. Therefore, all measurements in this study were made using non-destructive methods.

Vertical stratification and crown form

A total of 312 canopy-level trees are accessible using the canopy crane. Of these, 44 trees were chosen for crown measurements from four species, *P. menziesii*, *A. amabilis*, *A. grandis*, and *T. heterophylla* (Table 2.1). Together, these four species comprise 73% of the total number of trees with diameter at breast height ≥ 5cm in the 4ha study area (Freeman 1997). For each species, all trees accessible from the canopy crane were divided into 5m height classes, and 10% of the trees in each height class were chosen at random. The height of each foliated branch (> 0.5m in length) along the trunk of the tree was calculated using angle-distance measurements from the gondola of the canopy crane. Vertical distance from the gondola to the branch was calculated using a Laser Impulse Rangefinder (Laser Technology Inc., Englewood, CO, USA), and added to the height of the gondola above ground to determine height of the branch above ground. The following measures were calculated for each tree:

(1) Median branch height
(2) Lowest branch height
(3) Crown depth = tree height - lowest branch height
(4) Branch density = total number of foliated branches / crown depth

Crown expansion

Of the trees sampled for crown measurement, three trees were chosen from each species for measurements of shoot elongation and shoot production to compare rates of crown expansion. These represented large, medium and small canopy-level trees of each species (Table 2.2). The *P. menziesii* population consisted of larger trees than *A. amabilis, A. grandis*, and *T. heterophylla*, so the smallest sample of *P. menziesii* was larger than or similar in size to the large and medium sample trees of *A. amabilis, A. grandis*, and *T. heterophylla*. The live crown of each tree, from top of the tree to lowest foliated branch, was divided into three crown-levels of equal depth: upper-, mid-, and lower-crown. A branch which extended farthest away from the trunk was chosen near the mid-height of each crown-level.

The light environment at each branch was measured using the Sunfleck PAR Ceptometer (Decagon Devices Inc., Pullman, WA, USA), which uses several PAR sensors arranged in a line to calculate average photon flux density of PAR (photosynthetically active radiation) over a given area. Measurements at the branch and in a nearby field were taken simultaneously over a two-hour period around solar noon on an overcast day to obtain relative PAR.

Three terminal shoots farthest away from the trunk were chosen at each branch for terminal shoot elongation measurements (Figure 2.1A). Terminal shoot elongation over the past five years (1994-1999) was measured by following the terminal shoot basipetally and measuring the distances between annual budscale scars. These values were averaged to obtain the mean branch terminal shoot elongation rate per year.

Of the three branch terminal shoots chosen for elongation measurements, two were selected for shoot demography censuses. A branch map (Powell 1977, Stoll and Schmid 1998) was created by following each terminal shoot basipetally noting all annual budscale scars on the main axis and lateral branchlets as far back as live foliage was present on the main axis (Figure 2.1B). Each branch map took approximately 3 person-hours to complete. Sample size was limited to two branch maps per crown-level due to constraints on number of observers and time available for use of the canopy crane.

From autumn 1996 to spring 1999, shoot demography censuses were conducted twice per year: in early May before bud break (spring census), and in late October following the growing season and autumn needle fall (autumn census). At each census, the branches were compared with the branch maps from the previous census to determine rates of new shoot production and shoot mortality due to damage/loss and needle fall.

The following variables were calculated for the combined foliated shoots of the two branch maps at each crown-level:

(1) New shoot production rate (r):

$$r_T = n_{0.T} / n_{0.T-1}$$

where $n_{0.T}$ is the number of new shoots produced in year T.

(2) Net increase rate of all foliated shoots (R):

$$R_T = N_T / N_{T-1}$$

where N_T is the total number of foliated shoots of all age classes in year T. While r is a measure of annual shoot production during the growing season, R takes into account shoot mortality due to damage/loss and needle fall. R and r for each year of branch growth were averaged to obtain mean rates. These variables are based on those used in previous demographic studies of tree growth (Jones and Harper 1987, Maillette 1987).

Branching pattern

The final branch map for spring 1999 was used to characterize and compare branching patterns. The position of each lateral branchlet (secondary axis) growing from the main axis was identified by the main axis annual increment and position of the branchlet within the annual increment. For example, a lateral branchlet growing from the main axis at the seventh annual budscale scar from the terminal shoot was numbered 7-0, and branchlets basipetal from it on the same annual increment was numbered 7-1, 7-2, and so on (Figure 2.1B). Length of each lateral branchlet was measured from the base of the branchlet to the farthest point away from the main axis. This value was divided by the number of annual increments on the branchlet to obtain lateral branchlet elongation rate per year. In addition, bifurcation ratios for each year of lateral branchlet growth were calculated as follows (Kull et al. 1999):

$$Rb = n_k / n_{k+1}$$

where n_k is the number of shoots of age k. Bifurcation ratios for each year of lateral branchlet growth were averaged to obtain mean bifurcation ratio of the branchlet.

Results

Vertical stratification and crown form

Species comparisons of the vertical distribution of foliated branches within the crown elucidated general relationships between crown characteristics and tree height across species (Figure 2.2). Median branch height increased with increasing tree height for all species combined (Figure 2.2a, $r^2 = 0.924$, $P < 0.001$). Similarly, lowest branch height increased with increasing tree height ($r^2 = 0.215$, $P = 0.002$), but to a lesser extent than for median branch height. Comparison of median branch heights indicated that live crowns of *P. menziesii* mainly occurred in the upper canopy (40 - 60m) while those of *A. amabilis* mainly occurred in the mid (20 - 40m) to lower canopy (below 20m), resulting in vertical stratification of these two species. The live crowns of *A. grandis* and *T. heterophylla* occurred at all canopy levels. The lowest branch heights of all species occurred in the lower canopy, indicating that there is crown overlap among species in the mid to lower canopy.

To compare relative crown form among species, each variable was compared with tree height as a covariate. Median branch height did not differ among species when compared with tree height as a covariate (ANCOVA; $F = 1.603$, $P = 0.205$). Lowest branch height for *T. heterophylla* was significantly lower than for *P. menziesii* and *A. grandis* when compared with tree height as a covariate (ANCOVA: $F = 5.834$, $P = 0.002$). However, there were no differences in lowest branch height among *P. menziesii*, *A. amabilis* and *A. grandis* when compared with tree height as a covariate ($P > 0.05$). Crown depth increased with tree height for all species combined (Figure 2.2b: $r^2 = 0.872$, $P <$

0.001). Branch density decreased with increasing tree height for all species combined (Figure 2.2c, $r^2 = 0.696$, $P < 0.001$). *P. menziesii* had greater crown depth, and lower branch density compared with other species. However, when compared with tree height as a covariate, crown depth and branch density did not differ among species (ANCOVA: $F = 2.444$, $P = 0.079$; and $F = 1.270$, $P = 0.299$, respectively).

Crown expansion

Relative PAR decreased from upper- to lower-crown in all trees (Figure 2.3a). For all trees of *P. menziesii* and the large and medium trees of *A. amabilis*, *A. grandis*, and *T. heterophylla*, relative PAR decreased markedly from upper- to lower-crown. Changes in relative PAR from the upper- to lower-crown were small for the small trees of *A. amabilis*, *A. grandis*, and *T. heterophylla*.

For all trees of *P. menziesii*, the large trees of *A. amabilis*, *A. grandis*, and *T. heterophylla*, and the medium tree of *A. grandis*, branch terminal shoot elongation rates were consistently low (2.27 - 7.05 cm/yr) at all crown-levels despite large decrease in relative PAR from upper- to lower-crown (Figure 2.3b). In contrast, for the small trees of *A. amabilis*, *A. grandis*, and *T. heterophylla*, branch terminal shoot elongation rates were high (8.37 - 12.53 cm/yr) in the upper-crown and decreased markedly toward the lower-crown despite small decreases in relative PAR. The medium trees of *A. amabilis* and *T. heterophylla* showed intermediate trends between the large and small trees.

New shoot production rate (*r*) and net increase rate of all foliated shoots (*R*) generally decreased from upper- to lower-crown in most trees with the exception of the large tree of *T. heterophylla* where the opposite trend was observed (Figure 2.3c and d). For all trees of *P. menziesii* and for the large trees of *A. amabilis, A. grandis*, and *T. heterophylla*, changes in *r* and *R* from upper- to lower-crown were relatively small compared with the large decrease in relative PAR. Of these, the large tree of *T. heterophylla* showed the greatest change in *r* and *R* (1.30-1.65, 26.9% increase from upper- to lower-crown, and 1.37-1.62, 18.2% increase from upper- to lower-crown, respectively). The large tree of *A. amabilis* showed the least change in *r* and *R* (1.23-1.17, 4.9% decrease from upper- to lower-crown, and 1.19-1.14, 4.2% decrease from upper- to lower-crown, respectively). For the medium trees of *A. amabilis, A. grandis*, and the medium and small trees of *T. heterophylla*, decreasing trends in *r* and *R* from upper- to lower-crown corresponded well with decreases in relative PAR. Of these, the medium tree of *A. grandis* showed the greatest change in *r* (1.18-0.60, 49.2% decrease from upper- to lower-crown), while the medium tree of *T. heterophylla* showed the greatest change in *R* (1.69-1.05, 61.0% decrease from upper- to lower-crown). The medium tree of *A. amabilis* showed the least change in *r* and *R* (1.32-0.95, 28.0% decrease from upper- to lower-crown, and 1.20-1.05, 12.5% decrease from upper- to lower-crown, respectively). For the small trees of *A. amabilis* and *A. grandis*, *r* and *R* changed little from upper- to lower-crown as did PAR. The small tree of *A. amabilis* showed the greatest change in *r* (1.13-1.05, 7.1% decrease from upper- to lower crown), while the small tree of *A. grandis* showed the greatest change in *R* (1.16-0.96, 17.2%

decrease from upper- to mid-crown). The small tree of *A. grandis* showed the least change in R (1.11-1.04, 6.3% decrease from upper- to mid-crown), while the small tree of *A. amabilis* showed the least change in R (1.24-1.14, 8.1% decrease from upper- to lower-crown).

Branching pattern

Overall branching patterns were similar among *P. menziesii, A. amabilis* and *A. grandis*, in contrast to *T. heterophylla* (Figure 2.4). *P. menziesii, A. amabilis* and *A. grandis* generally had two to three lateral branchlets per main axis annual increment, and showed an excurrent branching pattern where lateral branchlet length increases basipetally along the main axis. *T. heterophylla* produced many more lateral branchlets per main axis annual increment than did *P. menziesii, A. amabilis* and *A. grandis*. The internodal lateral branchlets of *T. heterophylla* originate from axillary buds at internodal positions on the main axis and generally become shorter in length basipetally within each main axis annual increment. This pattern was strongest for the small tree. As a result, *T. heterophylla* shows a reiterating pattern in lateral branchlet length along the main axis where the distal branchlets on each main axis annual increment are longer than the proximal branchlets.

Relative frequency distributions of elongation rates and mean bifurcation ratios (*Rb*) of lateral branchlets were also similar among *P. menziesii, A. amabilis*, and *A. grandis*, in contrast to *T. heterophylla*. *P. menziesii, A. amabilis*, and *A. grandis* showed unimodal distributions of lateral branchlet elongation rates (Figure 2.5). The range of the distribution was narrower for *P.*

menziesii than for *A. amabilis* and *A. grandis*. In contrast, *T. heterophylla* showed a strongly positively-skewed distribution with numerous short lateral branchlets throughout all tree sizes and crown-levels. These results indicated less differentiation among lateral branchlets in their elongation rate for *P. menziesii*, *A. amabilis*, and *A. grandis*, and a clear differentiation between long and short lateral branchlets for *T. heterophylla*.

For *P. menziesii*, *A. amabilis*, and *A. grandis*, percentage of lateral branchlets whose mean bifurcation ratio (*Rb*) = 1 increased, and relative frequency distribution of bifurcation ratios became increasingly positively skewed from upper- to lower-crown (Figure 2.6). For *T. heterophylla*, more than 30% of branchlets in all crown-levels had mean *Rb* = 1, and the distributions were strongly positively-skewed for all trees and crown-levels. Maximum bifurcation ratios were lowest for *P. menziesii*, and slightly higher for *A. amabilis* and *A. grandis*. *T. heterophylla* had much higher maximum bifurcation ratios than *P. menziesii*, *A. amabilis*, and *A. grandis*. These results indicated less differentiation among lateral branchlets in their bifurcation ratio for *P. menziesii*, *A. amabilis*, and *A. grandis*, and a clear differentiation between lateral branchlets that produce only one new shoot each year and those that produce multiple shoots for *T. heterophylla*.

Discussion

I elucidated three canopy processes that may contribute to long-term coexistence of *P. menziesii* with late-successional species in old-growth *Pseudotsuga-Tsuga* forests. Comparison of vertical distribution of live crowns elucidated patterns of vertical stratification, and showed that *P. menziesii* crowns occur mainly in the upper canopy, above the crown of more shade-tolerant, late-successional species. Comparison of branch terminal shoot elongation rate and shoot production rates showed that crown expansion rate decreases in all species with increasing tree size, indicating crown competition is low among large trees in the upper canopy. Comparison of crown form showed that, because of their greater height, *P. menziesii* have deeper crowns and lower branch density than the shade-tolerant species. *P. menziesii* also has similar branching pattern with *A. amabilis* and *A. grandis*. Morphological characteristics of old-growth *P. menziesii* may be the result of acclimation to late-successional stand conditions. I propose that these three canopy processes, vertical stratification, low crown competition in the upper canopy, and morphological acclimation, contribute to long-term coexistence of *P. menziesii* with late-successional species in this forest. Below I review each of these processes in more detail.

Vertical stratification and crown form

Analyses of crown form elucidated some general relationships between crown characteristics and tree height that may represent convergence across species in crown form in response to prevailing stand conditions. Cody (1986) regards morphological convergence among plant species as a response to abiotic constraints that act similarly on all species, and divergence within these constraints as varied strategies for resource utilization. There was a clear separation between *P. menziesii* and *A. amabilis* in their respective crown positions within the canopy. Ishii et al. (2000) observed that *P. menziesii* dominates in the upper canopy of this forest in terms of tree height, and that *A. amabilis* is a mid- to lower-canopy species. The results of this study reinforced these observations by showing that live crowns of *P. menziesii* mainly occur in the upper canopy, while live crowns of *A. amabilis* mainly occur in the mid to lower canopy. The live crowns of *A. grandis* and *T. heterophylla* occurred at all canopy levels.

There was a convergent relationship between crown form and tree height across species. Along this relationship, *P. menziesii* have greater crown depth and lower branch density compared with other species. Deep crowns with fewer branches may allow more light to penetrate into the *P. menziesii* crown. This may be an efficient strategy for display of foliage area for relatively shade-intolerant *P. menziesii* growing in late-successional stand conditions. Most measures of crown form did not differ among species when compared with tree height as a covariate. However, *T. heterophylla* had lower lowest branch height relative to tree height compared with *P. menziesii* and *A. grandis* reflecting its high degree of relative shade-tolerance (Minore 1979).

Crown expansion

Analyses of shoot elongation and shoot production rates at the crown edge elucidated some general relationships between crown expansion rate and tree size across species. For all trees of *P. menziesii*, the large trees of *A. amabilis* and *T. heterophylla*, and the large and medium trees of *A. grandis*, branch terminal shoot elongation rates were low at all crown-levels, and relative changes in shoot production rates were small despite the marked decrease in relative PAR from upper- to lower-crown. All of these trees were taller than 45m in height. These results suggest that effects of physiological aging, sensu Clark (1983), and increasing size and complexity may be more important in controlling crown expansion rates in large trees than the local light environment. Decreasing growth rates with increasing age and size have been found for various tree species (Moorby and Wareing 1963, Borchert 1976, Jankiewicz and Stecki 1976, Ryan and Yoder 1997). Ishii et al. (2000) found that height-growth rates are also low in all trees of *P. menziesii* and the largest trees of the shade-tolerant species in this forest. These observations suggest that growth rates are low throughout the entire crown of large trees of all species and that height growth and crown expansion may have culminated.

In contrast, for small trees of *A. amabilis*, *A. grandis* and *T. heterophylla*, branch terminal shoot elongation rates were high in the upper-crown and decreased markedly toward the lower-crown, despite small decreases in light conditions. Changes in shoot production rates from upper- to lower-crown for these trees were small and corresponded to the small changes in PAR. Small trees of many conifers show excurrent crown form where shoot growth declines from upper- to lower-crown (Kozlowski and Ward 1961, Kozlowski 1971, Powell 1977, Ford et al. 1987). Small trees show high rates of branch terminal shoot elongation in response to small increases in light levels, suggesting that crown competition is intense, and that crown expansion into high-light areas of the upper canopy is important. Crown expansion under low light conditions may be more efficiently achieved by allocating to branch terminal shoot elongation than to shoot production.

The excurrent growth form observed for the small trees no longer occurs in *P. menziesii,* whose entire population in this stand consists of large trees, and in the large trees of *A. amabilis*, *A. grandis* and *T. heterophylla.* Decreased crown expansion rates throughout the crown in large trees may be the result of physiological limitations on growth due to their age, size and complexity (Ryan and Yoder 1997), and suggest that crown expansion has culminated. Decreasing crown expansion rates with increasing tree age and size across species indicates that crown competition decreases with increasing tree size. This may allow large trees of different species that survive the initial competitive exclusion stage to coexist in the upper canopy of this forest.

Branching pattern

The degree of differentiation between long and short lateral branchlets defined differences among species in their branching pattern. Despite differences in relative shade tolerance and successional status (Minore 1979), I found branching patterns to be similar among *P. menziesii*, *A. amabilis* and *A. grandis.* These three species have monopodial, determinate (preformed) shoot growth and display symmetrical branching patterns (Owens and Molder 1977, Oliver and Larson 1996). They have relatively simple branching pattern compared with *T. heterophylla* as evidenced by fewer internodal lateral branchlets along the main axis, and show less differentiation among branchlets in elongation rate and bifurcation ratio. *T. heterophylla* has potential for indeterminate (neoformed) shoot growth (Owens and Molder 1973, Powell 1991). High degrees of differentiation were found among lateral branchlets in their elongation rates and bifurcation ratio. Distal lateral branchlets within each main axis annual increment are long and have high bifurcation ratios. Maximum bifurcation ratios as high as 5.1 were found for branchlets that produce over 100 new shoots in four years of growth. Internodal lateral branchlets at proximal positions within each main axis annual increment are short and only produce one shoot in each year of growth. Similar branching patterns have been described for 30 to 50-year-old *T. heterophylla* in British Columbia (Owens and Molder 1973).

The symmetrical branching pattern and uniform shoot lengths, observed for *P. menziesii*, *A. amabilis* and *A. grandis*, produces very little overlap among shoots of plagiotropic branches, resulting in efficient foliage display for branches growing under low-light conditions. This type of efficient shoot and foliage display is most readily observed in the small trees of *A. amabilis* in the lower canopy. In contrast, differentiation between long and short lateral branchlets in *T. heterophylla* represents an alternative strategy for efficient foliage display for branches growing under low-light conditions. In a study of architectural plasticity in *Acer saccharum* Marsh. (sugar maple), Canham (1988) found that differentiation between long and short shoots in plagiotropic branches leads to efficient display of leaf area by minimizing overlap among leaves. Powell (1991) suggests that the potential for indeterminate shoot growth in species of *Tsuga* leads to high degrees of architectural plasticity. Short lateral branchlets of *T. heterophylla* fill in space between long lateral branchlets, resulting in efficient packing and display of foliage area.

The similarities in branching pattern among *P. menziesii*, *A. amabilis* and *A grandis* may represent convergence among species with determinate shoot growth to prevailing stand conditions. For *P. menziesii* this branching pattern is markedly different from young trees, and may be the result of morphological acclimation, as discussed in the following section. The differences between these three species and *T. heterophylla* represent divergence in strategies for shoot and foliage display. Both the symmetrical branching pattern observed for *P. menziesii*, *A. amabilis* and *A. grandis* and differentiation of long and short lateral branchlets observed for *T. heterophylla* can lead to efficient shoot and foliage display under low-light conditions by minimizing overlap among shoots on plagiotropic branches. This type of divergence in strategies for light capture may be an important mechanism for coexistence of *A. amabilis* and *T. heterophylla* in the low-light environment of the lower canopy. I observed many saplings and small trees of these two species growing adjacent to each other in this forest.

Implications for long-term coexistence of P. menziesii *with late-successional species*

Persistence of *P. menziesii* in old-growth *Pseudotsuga-Tsuga* forests and its long-term coexistence with late successional species may be realized by survival in the upper canopy above the crown of more shade-tolerant, late-successional species where crown competition is less intense. In addition, comparison of morphological characteristics of old-growth *P. menziesii* with studies on crown form and branching pattern of young and mature *P. menziesii* (less than 100 years old) in second-growth stands and plantations suggests that *P. menziesii* has high degrees of morphological plasticity that may allow it to acclimate to late-successional stand conditions.

Morphological characteristics of old-growth *P. menziesii* are markedly different from young and mature trees. Young *P. menziesii* trees grown in plantations have dense crowns with numerous internodal branches (Jensen and Long 1983). Branch densities range from 8 - 21 branches per vertical meter of trunk for 10- to 20-year-old *P. menziesii* (Maguire et al. 1994, St. Clair 1994, Kershaw and Maguire 1995). Bifurcation ratios range from 1.3 to 3.5 for young, open-grown *P. menziesii* trees (Mitchell 1974), and rates of vegetative bud production range from 1.6 to as high as 5.3 for 10- to 50-year-old trees (Owens 1969). Branch terminal shoot elongation rates for young *P. menziesii* branches range from 15 - 50 cm in 10- to 20-year-old trees (Brix and Ebell 1969, Owens et al. 1985, Webber et al. 1985), up to 10 times that of old *P. menziesii* trees in this study. These marked differences in crown form and branching pattern of old-growth *P. menziesii* compared with young and mature trees may be the result of physiological limitations on growth due to increasing age, size and complexity. They also reflect a high degree of morphological plasticity for *P. menziesii* that results in acclimation of crown form and branching pattern to late-successional conditions.

Vertical stratification, decreasing crown competition in the upper canopy, and morphological acclimation may be important canopy processes contributing to persistence of *P. menziesii* in old-growth *Pseudotsuga-Tsuga* forests, and to long-term coexistence of *P. menziesii* with late successional species. These processes define how *P. menziesii* functions in the old-growth forest canopy as a long-lived pioneer species.

Table 2.1. DBH, height and number of branches of trees sampled for crown measurement

Species	Number of trees sampled	DBH (cm)	Height (m)	Number of foliated branches
P. menziesii	10	72 - 148	46.2 - 64.8	64 - 191
A. amabilis	9	16 - 51	13.6 - 46.4	55 - 125
A. grandis	9	27 - 80	22.7 - 53.8	54 - 218
T. heterophylla	16	27 - 99	24.7 - 59.3	113 - 250

Table 2.2. DBH and height of large, medium and small trees of each species sampled for branching pattern, shoot elongation and shoot production.

Species	DBH (cm) / Height (m)		
	Large	Medium	Small
P. menziesii	166 / 64.8	148 / 57.5	72 / 46.2
A. amabilis	51 / 46.4	20 / 26.5	19 / 19.8
A. grandis	80 / 53.8	55 / 48.6	27 /30.5
T. heterophylla	93 / 53.3	51 / 42.1	27 / 24.7

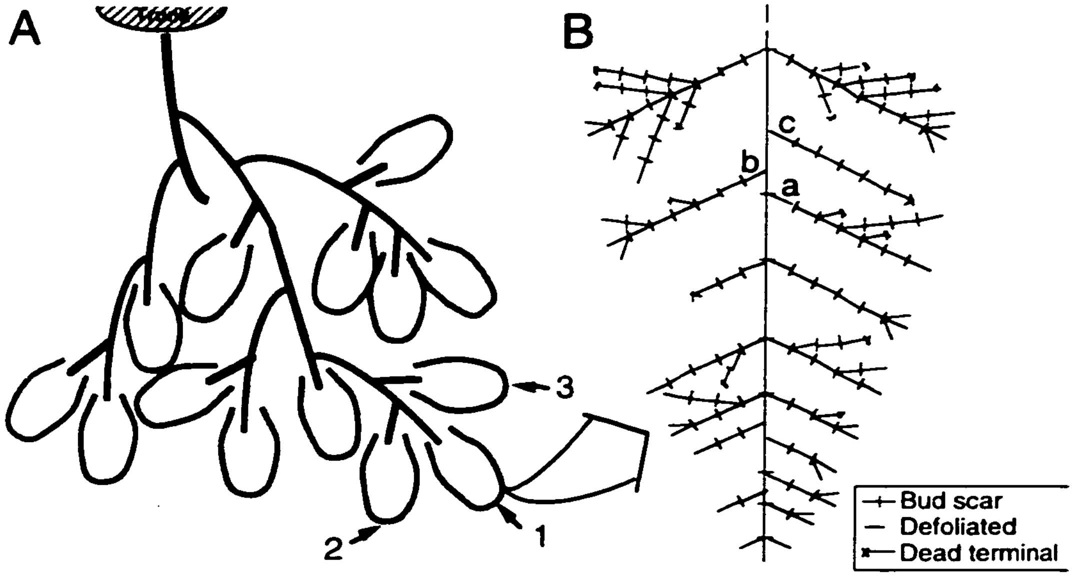


Figure 2.1. Schematic diagrams illustrating the sampling units. Three branch terminal shoots farthest away from the trunk (A, arrows 1-3) were selected for measurement of elongation rates. Of these, two were chosen for measurements of shoot demography and branching pattern using branch maps (B). The main axis was defined by following the branch terminal shoot basipetally as far back as foliage was present. The position of each lateral branchlet (secondary axis) growing from the main axis was identified basipetally by the main axis annual increment and position of the branchlet within the annual increment. For example branchlets a,b and c were numbered 7-0, 7-1 and 7-2, respectively. Shoot demography censuses were conducted twice yearly to document shoot production and mortality due to damage/loss and needle fall. Using the final branch map for spring 1999, position, elongation rate and bifurcation ratio of branchlets were measured to quantify branching pattern.

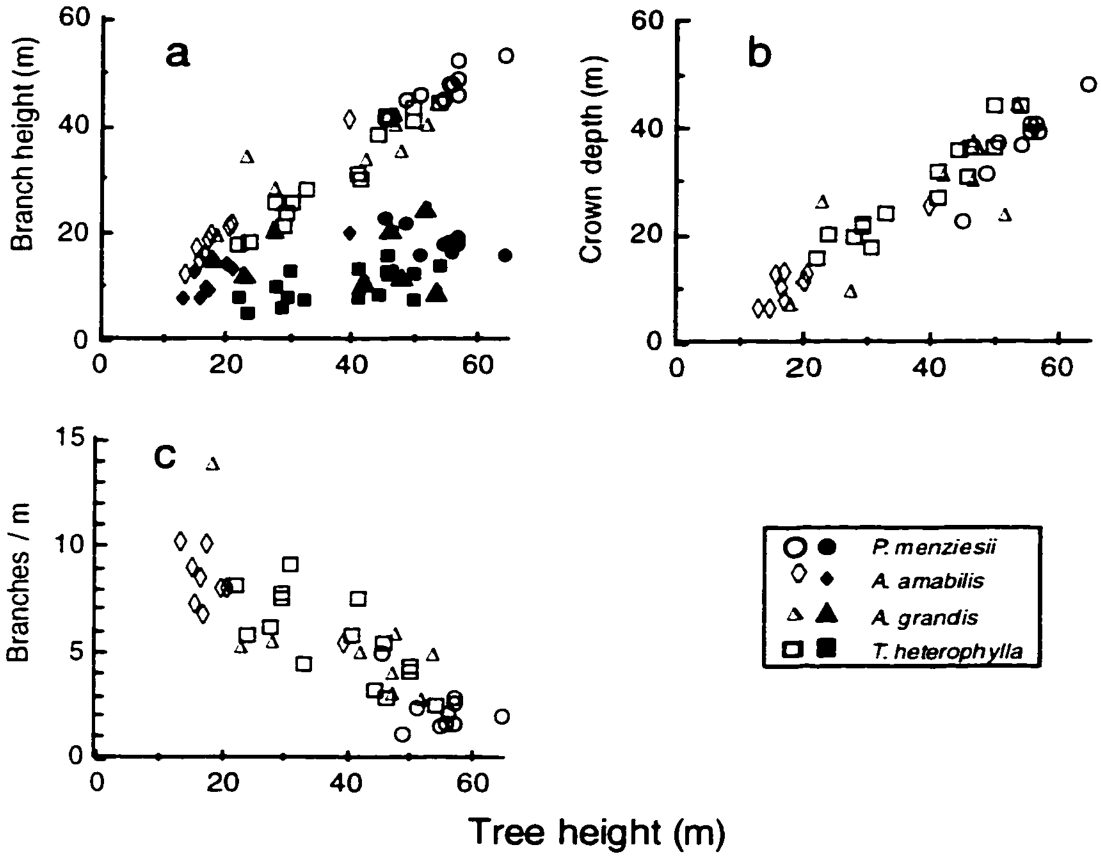


Figure 2.2. Relationships between median branch height (a: open symbols), lowest branch height (a: filled symbols), crown depth (b), and branch density (c) with tree height. Filled and open symbols with the same tree height in (a) represent median and lowest branch heights of the same tree.

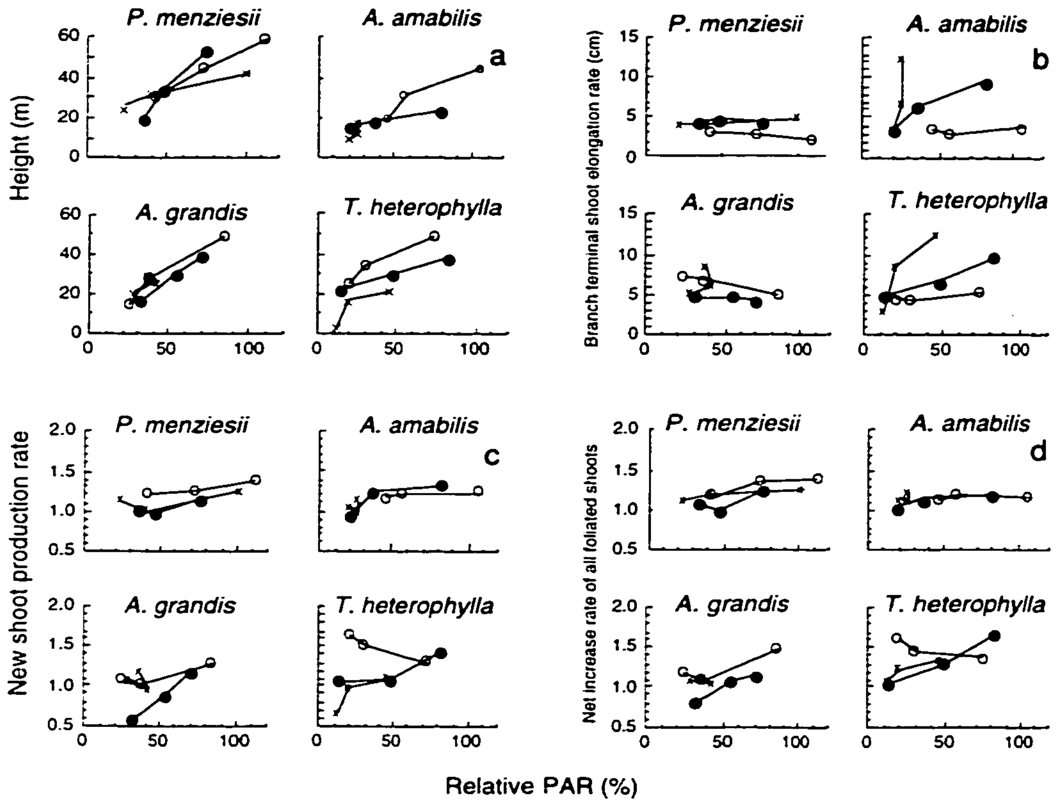


Figure 2.3. Relationships between relative PAR and branch height (a), branch terminal shoot elongation rate (b), new shoot production rate (c), net increase rate of all foliated shoots (d) for large (O), medium (●) and small (X) trees of each species.

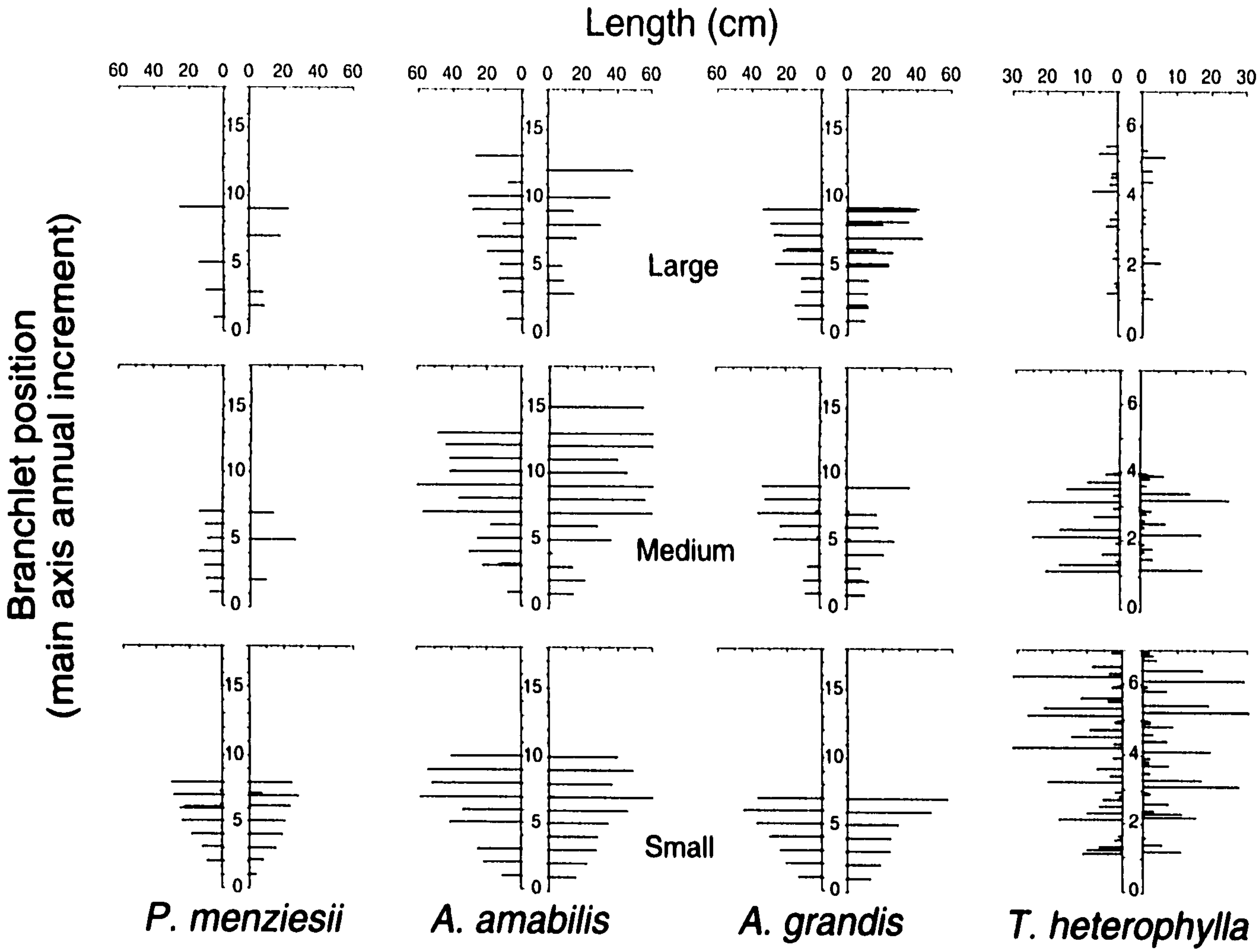


Figure 2.4. Length and position of lateral branchlets along the left and right sides of the main axis of the branch tip, illustrating branching patterns for the upper-crown branches of large, medium and small trees of each species. Note different axis scales for *T. heterophylla*.

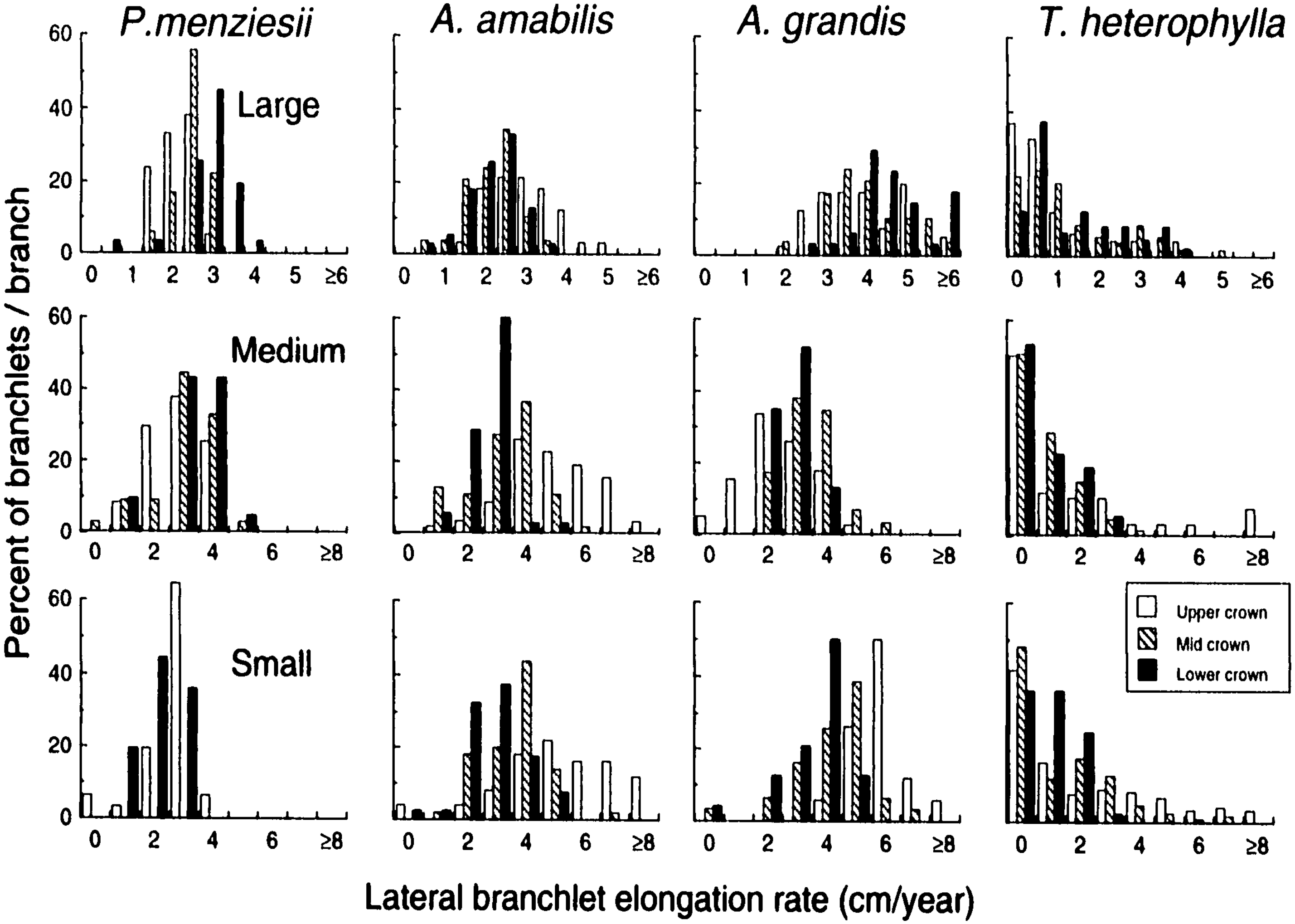


Figure 2.5. Relative frequency distributions of lateral branchlet elongation rates. Note different x-axis range and intervals for elongation rates of the large trees of each species. Elongation rates for the mid-crown branch of the small tree of *P. menziesii* could not be obtained due to damage to the branch in winter of 1999.

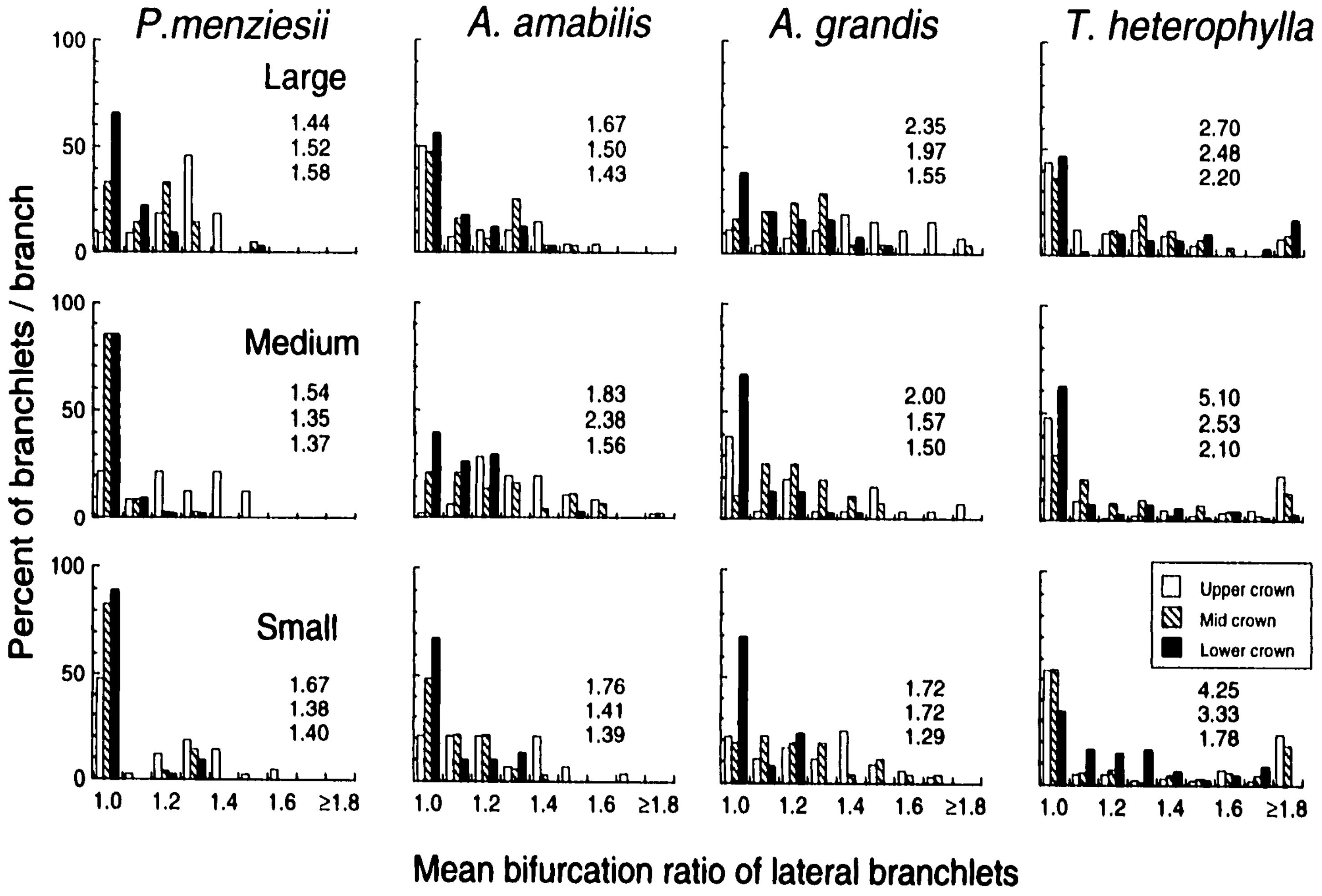


Figure 2.6. Relative frequency distributions of mean bifurcation ratios (*Rb*) of lateral branchlets. Numbers indicate maximum mean *Rb* observed for upper-, mid- and lower-crown branches, respectively, of each tree. Mean *Rb* for the mid-crown branch of the small tree of *P. menziesii* is based on data from 1996 to 1998 (one year less than for the other branches) due to damage to the branch in winter of 1999.

CHAPTER III

The role of epicormic shoot production in maintaining foliage in old-growth *Pseudotsuga menziesii* (Douglas-fir)

Introduction

Old-growth temperate forests of the Pacific Northwest Coast of North America, have some of the largest and longest-living coniferous trees in the world (Waring and Franklin 1979). Following large-scale disturbance, forest succession in mid-elevation coniferous forests of this region generally proceeds from initial dominance by *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* (coastal Douglas-fir) to later invasion by late-successional species such as *Tsuga heterophylla* (Raf.) Sarg. (western hemlock), *Thuja plicata* Donn ex D. Don (western red cedar), *Abies amabilis* Dougl. ex Forbes (Pacific silver fir), and *Taxus brevifolia* Nutt. (Pacific yew) (Munger 1940, Franklin and Hemstrom 1981, Spies and Franklin 1989, Stewart 1989). Although, *P. menziesii* is considered a pioneer species, individual trees can live over 1000 years and persist in the forest for centuries, well into later stages of succession. In a study of a 450-year-old *Pseudotsuga-Tsuga* forest in this region, In Chapter 2, I proposed that sustained dominance in the upper canopy combined with architectural acclimation in later stages of succession may contribute to long-term survival of *P. menziesii*. In addition, *P. menziesii* in the stand have reached their maximum attainable height (Ishii et al. 2000) and crown expansion has culminated (Chapter 2). In their population dynamics study of the same stand, Franklin and DeBell (1988) predict that, if current mortality rates continue, *P. menziesii* would continue to persist in the forest for an additional 755 years. However, it is not clear how individual trees of *P. menziesii* continue to survive after height growth and crown expansion have culminated.

In his review of tree longevity and aging, Westing (1964) conceded that meristematic cells of trees may have potential for infinite growth, and attributed causes of physiological aging, sensu Clark (1983), to increase in respiratory demands, accumulation of inhibitory substances, and vulnerability to pathogens. Connor and Lanner (1990) found no apparent difference in cambial cell production among young and old (4000+ years old) trees of bristlecone pine (*Pinus longaeva* D.K. Bailey), and concluded that tree death in this species may occur from external rather than internal causes. Westing (1964) also noted that meristematic cells can lie quiescent for some years in the form of dormant buds and suggested that production of epicormic shoots from such buds would forestall the effects of aging and rejuvenate the tree. Bryan and Lanner (1981) found that epicormic branching in Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) is a "natural habit of replacing dead and dying crown components" and contributes to prolonging tree longevity. Remphrey and Davidson (1992) found that epicormic shoot production in branches of green ash (*Fraxinus pennsylvanica* var. *subintegerrima* (Vahl) Fern.) contributed to maintaining productivity by increasing foliage area in older, inner regions of the crown. Other researchers have suggested similar effects of epicormic shoot production on tree longevity and maintenance of productivity (Ewers 1983, Bégin and Fillion 1999).

Epicormic shoots (Figure 3.1) originate from dormant preventitious buds and secondary daughter buds that proliferate from them (Kozlowski 1971, Zimmermann and Brown 1971). Epicormic shoot production has been more extensively studied in hardwoods (e.g. Kormanik and Brown 1969, Kauppi et al. 1987, Burrows 1990, Ito 1996), but has also been found to occur in conifers (e.g. Stein 1955, Bryan and Lanner 1981, Connor and Lanner 1986, Bégin and Fillion 1999). Epicormic shoot production often occurs in response to exogenous stimuli such as pruning, damage and defoliation, or increased light, water and nutrients (Zimmermann and Brown 1971, Hallé et al. 1978). However, numerous studies have found no apparent causal factor directly related to the production of epicormic shoots in many species and suggested that there may be an inherent natural pattern to their production (Bryan and Lanner 1981, Connor and Lanner 1986, Remphrey and Davidson 1992, Ito 1996, Bégin and Fillion 1999).

Bégin and Filion (1999) found that epicormic shoot production resulted in reiteration of basic architectural units in black spruce (*Picea mariana* (Mill.) BSP). Reiteration is a process whereby architectural units are duplicated within the tree from dormant buds (proleptic reiteration) or from growing axes (sylleptic reiteration) (Hallé et al. 1978). Bégin and Filion (1999) also distinguish "traumatic reiteration" that occurs in response to exogenous stimuli and "adaptive reiteration" that occurs in response to physiological needs as part of the normal development of the tree. Bégin and Filion (1999) observed adaptive proleptic reiteration in early stages of development in black spruce on ca. 10-year-old branches, and proposed that it is an important strategy for maintaining photosynthetic capacity.

I observed ubiquitous adaptive proleptic reiteration in the form of constant production and growth of epicormic shoots in crowns of 400-year-old *P. menziesii* trees. In this study, I characterize architectural units and amounts of shoots and foliage on branches that are reiterated as a result of this process, and discuss the role of epicormic shoot production in maintaining foliage in established crowns of old *P. menziesii* trees. I also discuss the implications of adaptive proleptic reiteration for persistence of individual trees of this species in old-growth coniferous forests of the Pacific Northwest Coast of North America.

Study site and methods

The study was conducted in an old-growth *P. menziesii - T. heterophylla* forest at the Wind River Canopy Crane Research Facility located in the Thornton T. Munger Research Natural Area, Gifford Pinchot National Forest in southwestern Washington State, USA. (45°49'N, 121°57'W; altitude 355m). The stand basal area is dominated by *P. menziesii* and *T. heterophylla*. *T. plicata*, *A. amabilis* and *T. brevifolia* are also abundant. Other tree species in the stand include: *Abies grandis* (Dougl. ex D. Don) Lindl. (grand fir), *Pinus monticola* Dougl. ex D. Don (western white pine), and *Cornus nuttalii* Audubon (Pacific dogwood). Franklin (1972) and Franklin and DeBell (1988) give a detailed description of the area.

Destructive sampling within the Research Natural Area is restricted. Permission was obtained to sample nine branches from three trees representing large, medium and small *P. menziesii* trees in the stand in terms of tree height (here after: Tall Tree, Medium Tree, and Short Tree, Table 3.1). The trees are believed to have established after a stand-replacing major disturbance in the area (Franklin and DeBell 1988). Tree age at breast height was estimated from increment cores, and were 415 years for the Tall Tree and 405 years for the Short Tree. The Medium Tree could not be successfully aged. Other *P. menziesii* trees in the area ranged in age from 385 to 410 years old at breast height.

The three sample trees were climbed in August of 1998 using the single-rope technique (Lilly 1998, Clement and Shaw 1999), for measurement of crown characteristics. All primary branches were numbered, and branch height above ground was measured using a tape measure that was stretched vertically from the ground along the trunk of each tree. Branch diameter was measured immediately outside the branch collar using diameter tape for large branches and calipers for small branches. Branch length was measured by extending a one-inch-wide engineer's tape from the trunk to the farthest foliated section of the branch. The top 2 - 3m of each tree was not climbed for safety reasons. The live crown of each tree, from the top of the tree to the lowest foliated branch, was divided into upper-, mid-, and lower-crown levels of equal depth. A median sized branch, in terms of diameter and length, was cut near the mid-height of each crown level (here after: upper-, mid-, and lower-crown branches). The branches were carefully lowered to the ground using ropes so as to not damage them and then transported to a nearby building for additional measurements.

The age of each harvested branch was estimated by counting the number of annual rings at the base of the branch, with the awareness that this may underestimate branch age as *P. menziesii* branches can have missing rings, especially in branches growing under low-light conditions of the lower-crown (Reukema 1959, Kershaw et al. 1990). The foliated shoots on each harvested branch were divided into 'shoot cluster units'. A shoot cluster unit (SCU) is an architectural unit of shoot organization formed as a result of the symmetrical branching pattern observed in old *P. menziesii* trees (Figure 3.2). The terminal bud usually forms one terminal shoot and two to three lateral shoots each year. As a result, shoots are organized in clusters consisting of a distinguishable main axis, created by the extending terminal shoot, and several lateral branchlets. The morphology of the SCU is similar to a compound leaf with the main axis analogous to the rachis and lateral branchlets to individual leaflets. In addition to regular production of terminal and lateral shoots, epicormic shoots are produced along the main axis of the SCU (Figure 3.1) and grow to form epicormic branchlets.

Epicormic branchlets can be distinguished because they (1) originate from internodal positions on older main axis parent shoots, (2) grow out at vertical angles above the plain formed by the main axis and regular lateral branchlets, and (3) are younger than the annual daughter shoots of the same main axis parent shoot. Many SCUs are comprised of "regular shoots" forming the main axis and regular lateral branchlets, and subsequently produced "epicormic shoots" forming epicormic branchlets. While terminal buds of regular branchlets usually only produce one to two new shoots per year, terminal buds of epicormic branchlets often produce three or more new shoots and form the basis of new SCUs. Age of SCUs can be determined by counting the number of annual budscale scars along the main axis. A newly forming SCU was considered as part of the parent SCU if its age was younger than the maximum foliage longevity, and all shoots along the main axis were foliated. A new SCU was considered independent from its parent unit if it was older than the maximum foliage longevity, and had developed a petiole-like section at the base of the main axis separating its foliated shoots spatially from the parent SCU. Many SCUs had younger SCUs originating from epicormic shoots produced along the main axis that were still not independent from the parent unit.

All SCUs on the sample branches were numbered, and radial distance from the branch base to the base of each SCU (here after: SCU position) was measured before removing it from the branch. After removal, the SCU was laid flat, and length and width of the foliated section, and diameter at the base of the main axis were measured using ruler and calipers. Age of the SCU was determined by counting annual budscale scars along the main axis to the base of the SCU. All foliated shoots on the SCU were aged using budscale scars and separated into regular and epicormic shoots by age-class.

Frequency and timing of epicormic shoot production

Frequency of epicormic shoot production was investigated by comparing among branches percentages of SCUs with epicormic branchlets and number of epicormic branchlets produced per SCU. Timing of epicormic shoot production was determined by comparing the age of each epicormic branchlet to age of the main axis parent shoot from which it had originated. For example, a four-year-old epicormic branchlet growing out of a ten-year-old parent shoot indicates that the epicormic branchlet was produced when the parent shoot was six years old. This is equivalent to the amount of time the epicormic bud was dormant on the parent shoot. Frequency and timing of epicormic shoot production were taken for all branches except for the lower-crown branch of the Tall Tree. This branch was the first to be cut, and the sampling design for this part of the study was not complete at this time.

Growth and development of the SCU

The age structures of regular and epicormic shoots in each SCU were used to characterize five phases of SCU development. The percentage of SCUs in each branch belonging to each phase of SCU development was calculated. SCU characteristics such as size and age were compared among these phases.

To characterize morphological development of SCUs, I calculated ages of SCUs when epicormic branchlets were produced by subtracting the age of each epicormic branchlet from the age of the SCU. In addition, all SCUs on branches of the Medium Tree were mapped (Figure 3.3). For each SCU, measurements were taken of all regular lateral branchlets and epicormic branchlets: distance from the distal end of the main axis, length, and presence or absence of a live terminal bud. Morphological characteristics were compared among phases of SCU development to infer the morphological development of SCUs.

Effects of epicormic shoot production on shoot and foliage dynamics

For one-half of the SCUs in each branch, 10% (minimum three shoots) of the shoots in each shoot age-class for both shoot types (regular / epicormic) were preserved for subsequent foliage area measurement (foliage-area samples), while remaining shoots were dried for foliage weight measurement (dry-weight samples). All needles of the remaining one-half of the SCUs were sorted by shoot age-class and shoot type, and oven-dried at 70°C until constant weight was reached (usually 2-3 days), and weighed to determine foliage dry mass.

Foliage area was measured by removing all needles on the foliage-area sample shoots and laying them out on a computer scanner (UMAX 1200S, UMAX Corp., Fremont, CA, USA). The needles were flattened with a piece of glass, lighted from above to obtain the silhouette, and scanned at 300 dpi resolution. The scanned images were processed using Scion Image (Scion Corp., Frederick, MD, USA) image analysis program to obtain one-sided needle area to the nearest 0.1 cm^2. Relative error for this method was estimated to be less than 2%. The needles were then oven-dried for foliage weight measurement.

Needles from the foliage-area samples and dry-weight samples were oven-dried at 70°C until constant weight was reached. Weight of the foliage-area samples was used to determine specific needle area (SNA; cm^2 / g) for each shoot age-class and shoot type. The weights of the foliage-area sample and dry-weight sample were added for each SCU to determine total foliage dry mass for each shoot age-class and shoot type.

SNA increased from upper- to lower-crown branches, and decreased with increasing SCU position (radial distance from the branch base, Figure 3.4).

There was a significant negative relationship between SNA and SCU position for most shoot age-classes and shoot types. Linear regressions of the form:

[1] $$\text{SNA} = a\,x + b$$

where x is SCU position and a and b are parameters, were fit for each shoot age-class and shoot type. A set of regressions were developed for each branch, and used to estimate SNA of each shoot age-class and shoot type from SCU position for SCUs where foliage-area samples were not taken. For shoot age-classes and shoot types where this relationship was not significant, mean SNA of the age-class and shoot type for the branch was used. By multiplying the measured and estimated SNAs by foliage dry mass, total foliage area was determined for each shoot age-class and shoot type for all SCUs.

The amounts of shoots and foliage born on regular and epicormic shoots were calculated for each branch. In addition, the amounts of shoots and foliage comprising SCU of various ages were compared among branches to infer branch growth and development from dynamics of SCUs. Previous studies have applied this type of demographic approach to inferring tree growth pattern from dynamics of modular units such as buds, shoots and foliage, (e.g. Maillette 1982, Jones and Harper 1987, Wilson 1989). However, buds, shoots and foliage are not independent units, and their dynamics have the confounding influence of morphological constraints such as branching pattern. Reiterating architectural units, such as SCUs in this study, are more independent units and may be more appropriate for use in demographic analyses (Bégin and Fillion 1999).

Results

Frequency and timing of epicormic shoot production

For all trees, mid-crown branches had much greater total numbers of SCUs than upper- and lower-crown branches (Table 3.2). Epicormic shoot production was observed in 56.8% to 100% of SCU on branches. This percentage increased from upper- to lower-crown branches in the Tall Tree and Medium Tree. For the Short Tree, the mid-crown branch had a slightly lower percentage than the upper-crown branch.

Mean frequency of epicormic shoot production ranged from 2.57 (upper-crown branch, Tall Tree) to 8.36 (lower-crown branch, Short Tree) branchlets per SCU, and did not differ among branches with the exception of the mid-crown branch of the Tall Tree and the lower-crown branch of the Short Tree, both of which had higher values than other branches on the same tree (Table 3.2). Frequency of epicormic shoot production in each SCU was positively correlated with SCU size (length x width of the foliated section) and SCU diameter (at the base of the main axis) in all branches, and with SCU age in 7 of 8 branches. Frequency of epicormic shoot production was not consistently correlated with SCU position. This indicated that larger, older SCUs have more epicormic branchlets than smaller, younger SCUs, but the occurrence of epicormic branchlets did not vary with SCU position within the branch.

Mean timing of epicormic shoot production ranged from 5.08 (lower-crown branch, Medium Tree) to 7.02 (mid-crown branch, Short Tree) years, and did not differ among branches in all trees with the exception of the mid-crown branch of the Short Tree where it was greater than for the upper- and lower-crown branches (Table 3.2). Timing of epicormic shoot production was positively correlated with SCU size in 5 of 8 branches, and with SCU age in 6 of 8 branches, but was not consistently correlated with SCU diameter and position. This indicated that epicormic buds remain dormant for longer periods in larger, older SCUs, but the period of dormancy does not change with SCU position within the branch. However, correlation coefficients for timing of epicormic shoot production were relatively low, indicating that the relationships are not strong.

Growth and development of the SCU

Based on age structures of regular and epicormic shoots comprising each SCU, five phases of SCU development were identified (Figure 3.5). Age structures of regular and epicormic shoots were distinguished as "expanding" where number of shoots in each age class successively increases toward younger age classes, or "declining" where number of shoots in each age class increases and then decreases or remains constant toward younger age classes. Based on these criteria, SCUs were distinguished into three phases of growth and reiteration, and two phases of decline.

The three phases of growth and reiteration are:

- Regular Growth Phase: The SCU consists only of regular shoots showing an expanding age structure. This is the first phase of SCU development.
- Epicormic Initiation Phase: The SCU consists of both regular and epicormic shoots, and both types of shoots show expanding age structures. This phase is observed when the SCU first start to develop epicormic branchlets.

- Epicormic Renewal Phase: The SCU consists of both regular and epicormic shoots, and regular shoots show an declining age structure, while epicormic shoots show an expanding age structure. This phase is observed when the parent SCU begins to decline after further development of epicormic branchlets.

The two phases of decline are:

- Decline 1 Phase: The SCU consists only of regular shoots showing a declining age structure. This phase is observed when the SCU declines without producing epicormic branchlets or after newly formed SCUs originating from epicormic branchlets become independent and the declining parent SCU has no other epicormic branchlets.
- Decline 2 Phase: The SCU consists of both regular and epicormic shoots, and both types of shoots show declining age structures. This phase is observed when both epicormic branchlets and the parent SCU decline after the Epicormic Initiation Phase or Epicormic Renewal Phase.

The percentage of SCUs in the five phases of SCU development changed with branch position (Figure 3.6). Upper-crown branches had high percentages of SCUs in Regular Growth Phase and Epicormic Initiation Phase, and low percentages in the two phases of decline. Together, Regular Growth Phase and Epicormic Initiation Phase accounted for 85% (Tall Tree), 58% (Medium Tree), and 68% (Short Tree) of SCUs of upper-crown branches, while the two phases of decline accounted for only 8% (Tall Tree), 21% (Medium Tree) and 5% (Short Tree). Mid- and lower-crown branches had high percentages of SCUs in Epicormic Initiation Phase and Epicormic Renewal Phase, and relatively high percentages in the two phases of decline. Together, Epicormic Initiation Phase and Epicormic Renewal Phase accounted for 56% (Tall Tree), 57% (Medium Tree), and 46% (Short Tree) of SCUs of mid-crown branches, and 57% (Tall Tree), 80% (Medium Tree), and 61% (Short Tree) of SCUs of lower-crown branches. The two phases of decline accounted for 38% (Tall Tree), 43% (Medium Tree) and 47% (Short Tree) of SCUs of mid-crown branches, and 43% (Tall Tree), 19% (Medium Tree), and 32% (Short Tree) of SCUs of lower-crown branches.

Size and age of SCUs were related to phases of SCU development and to branch height. These trends were most apparent for the Tall Tree (Figure 3.7). When compared across the five phases of SCU development, there was an increasing trend in mean number of shoots and mean SCU age from Regular Growth Phase to Epicormic Initiation Phase and Epicormic Renewal Phase. Mean number of shoots per SCU was lower for the two phases of decline compared with the three phases of growth and reiteration, while SCU ages were similar. When compared across branches, there was an increasing trend in mean number of shoots per SCU and mean SCU age from upper- to lower-crown branches within each phase of SCU development, with the exception of the Regular Growth Phase. This suggested that SCU sizes are smaller and SCUs develop more rapidly in upper-crown branches, than in lower-crown branches. Similar trends were observed for the Medium Tree and Short Tree.

SCUs began producing epicormic branchlets at ages as young as 3 - 4 years old (Figure 3.8). The highest percentage of epicormic branchlets were produced when SCU were 7 - 12 years old. In general, epicormic branchlets were produced at younger ages in SCU of upper-crown branches than those of lower-crown branches. For example, modes of the distribution for upper-, mid- and lower-crown branches of the Short Tree were, 6-7, 8-9, and 12-13 years, respectively. This suggested that SCUs develop more rapidly in upper-crown branches than in lower-crown branches.

Measurements on SCU morphology were taken for branches of the Medium Tree, and trends in SCU morphology with phases of SCU development were most apparent for the mid-crown branch (Figure 3.9). In the Regular Growth Phase, regular lateral branchlets occurred near the distal end of main axes of SCUs, and all had live terminal buds. In the Epicormic Initiation Phase, regular lateral branchlets occurred toward the distal end of main axes, while epicormic branchlets occurred at more proximal positions. Percentage of regular lateral branchlets with live terminal buds decreased from 100% to 0% with increasing distance away from the distal end of main axes, while for epicormic branchlets, percentages decreased from 100% to 55% and then increased to 100%. In the Epicormic Renewal Phase, distributions of regular and epicormic branchlets were similar to the Epicormic Initiation Phase with epicormic branchlets occurring more toward the proximal end of main axes than regular lateral branchlets. Percentage of regular lateral branchlets with live terminal buds decreased from 74% to 0% with increasing distance away from the distal end of main axes, while for epicormic branchlets, it decreased from 100% to 33% and then increased to 100%. In both the Epicormic Initiation Phase and Epicormic Renewal Phase, the mode of distribution of epicormic branchlets corresponded to the position along main axes where percentage of regular lateral branchlets with live terminal buds neared 50%; 40 - 50 cm for the Epicormic Initiation Phase and 30 - 40 cm for the Epicormic Renewal Phase. In the Decline 1 Phase, regular lateral branchlets occurred more toward the distal end of main axes compared with the Regular Growth Phase, and percentage of branchlets with live terminal buds decreased rapidly from 100% to 0% with increasing distance from the distal end of main axes. In the Decline 2 Phase, distributions of regular and epicormic branchlets were similar to the Epicormic Initiation Phase and Epicormic Renewal Phase with epicormic branchlets occurring more toward the proximal end of main axes than regular lateral branchlets. Percentage of regular lateral branchlets with live terminal buds decreased from 40% to 0% with increasing distance away from the distal end of main axes, while for epicormic branchlets, it decreased from 75% to 22% and then increased to 100%. Similar changes in SCU morphology with phases of SCU development were observed for the upper- and lower-crown branches.

To summarize the development of SCUs, upper-crown branches have more SCUs in the Regular Growth Phase and the Epicormic Initiation Phase, while mid- and lower-crown branches have more SCUs in the Epicormic Initiation Phase, the Epicormic Renewal Phase, and in the two phases of decline. SCU size increases as SCUs increase in age and progress from Regular Growth Phase to Epicormic Initiation Phase and Epicormic Renewal Phase. However, SCUs may decline at various ages during their development. Mean size and age of SCUs were smaller and younger for upper-crown branches than for lower-crown branches, suggesting that SCUs are smaller and develop more rapidly in upper-crown branches. SCUs began producing epicormic branchlets as young as 3-4 years old and there was a peak to the production of epicormic branchlets at 7-12 years. Upper-crown branches produced epicormic branchlets at younger ages than did lower-crown branches, suggesting that SCUs develop more rapidly in upper-crown branches. Epicormic branchlets occur at more proximal positions along main axes of SCUs relative to regular lateral branchlets. In addition, epicormic branchlets produce new shoots at positions where more than 50% of regular lateral branchlets are no longer producing new shoots. Changes in SCU morphology as epicormic branchlets grow to replace regular lateral branchlets can be observed by comparing the Regular Growth Phase, Epicormic Initiation Phase, Epicormic Renewal Phase and Decline 2 Phase (Figure 3.9).

Effects of epicormic shoot production on shoot and foliage dynamics

Percentages of shoots and foliage produced by epicormic shoots increased from upper- to lower-crown branches for the Tall Tree and the Medium Tree (Table 3.3). For the Short Tree, percentages were lowest for the mid-crown branch compared with the upper- and lower-crown branches. Of the nine sample branches, the upper-crown branch of the Tall Tree had the lowest percentage (9.9% of shoots, 7.0% of foliage dry mass, and 8.0% of foliage area) and the lower-crown branch had the highest percentage (49.8% of shoots, 46.0% of foliage dry mass, and 48.1% of foliage area). For all branches, percentages of current-year shoots and foliage produced by epicormic shoots were higher than for all shoots combined, ranging from 11.4% to 66.0% of current-year shoots, 8.1% to 64.6% of current-year foliage dry mass, and 9.4% to 48.1% of current-year foliage area.

The mode of the relative distribution of shoots, foliage dry mass, and foliage area across SCU age-classes increased from upper- to lower-crown branches (Figure 3.10). This trend was strongest for the Tall Tree whose upper-crown branch had a mode at 10-11 years for number of shoots, and 6-7 years for foliage dry mass and foliage area, while mid- and lower-crown branches had modes at 12-13 years for shoots, foliage dry mass, and foliage area. Similar trends were observed for the Medium Tree and Short Tree.

Discussion

Epicormic shoot production in crowns of old *P. menziesii* trees is a constant process that occurs in branches from different parts of the crown and in trees of different sizes. This suggests that epicormic shoot production in old *P. menziesii* trees is not a response to exogenous stimuli, but a natural part of branch growth and development. Epicormic shoot production results in adaptive reiteration of SCUs and maintenance of shoots and foliage on branches of old *P. menziesii* trees.

Frequency and timing of epicormic shoot production

If epicormic shoot production were caused by exogenous stimuli such as damage, one would expect upper-crown branches which are more exposed to harsh environments to have higher frequency of epicormic shoot production. However, frequency of epicormic shoot production was not higher for upper-crown branches compared with mid- and lower-crown branches. In addition, frequency of epicormic shoot production did not vary with SCU position within the branch. These results suggest that epicormic shoot production in old *P. menziesii* trees occurs without exogenous stimuli.

If epicormic shoot production were caused by exogenous stimuli, the timing of epicormic shoot production should also vary among upper- and lower-crown branches depending on the degree of damage or other stimuli. However, timing of epicormic shoot production was relatively constant from upper- to lower-crown branches. In addition, timing of epicormic shoot production did not vary with SCU position within the branch. These results show that the number of years epicormic buds remain dormant is not affected by crown position, and that release of epicormic buds from dormancy occurs without exogenous stimuli.

Growth and development of the SCU

Distinguishing regular and epicormic shoots comprising each SCU helped identify phases of SCU development and elucidate morphological development of SCUs. Differences among branches in percentages of SCUs in the five phases of SCU development reflected differences in SCU dynamics. Upper-crown branches are smaller and younger than mid-crown branches, and have high percentages of SCU in early phases of growth and reiteration. This suggests that SCUs of upper-crown branches are still expanding and the branch as a whole is still growing in size. Mid-crown branches were larger and older, and had high percentages of SCUs in late phases of growth and reiteration, and relatively high percentages in the two phases of decline. This suggests that many SCUs are no longer expanding, indicating that mid-crown branches are further developed than upper-crown branches, and may have reached maximum size.

The differences between upper- and mid-crown branches show that, as branches develop in size and branch growth declines, more SCUs are reiterated by epicormic shoot production. Lower-crown branches also had higher percentages of SCUs in late phases of growth and reiteration, and relatively high percentages in the two phases of decline. These branches were relatively small in size and varied in age. Growth of lower-crown branches may also be declining due to the low-light environment of the lower crown, resulting in more frequent production of epicormic shoots and adaptive reiteration of SCUs.

Investigation of the morphological development of SCUs showed that the expanding branching pattern of regular shoots results in the expanding age-structure in the Regular Growth Phase (Figure 3.11). From the Regular Growth Phase, epicormic branchlets may be produced along main axes of SCUs while regular lateral branchlets are still growing, and the SCU develops to the Epicormic Initiation Phase (Figure 3.11, a). SCUs begin producing epicormic branchlets as early as 3 to 4 years in age. The greatest number of epicormic branchlets are produced when SCUs were 7 - 12 years old, and epicormic branchlet production declines thereafter, suggesting that SCUs may decline in vigor after producing epicormic branchlets. Epicormic branchlets occur toward the proximal end of main axes in areas where most of the regular lateral branchlets are no longer producing new shoots. SCUs were found in the Decline 1 Phase at ages as early as 6 years, suggesting that some SCUs may also decline without producing any epicormic branchlets (Figure 3.11, b). From the Epicormic Initiation Phase, shoot production rates of regular lateral branchlets may decline, while epicormic branchlets maintain high shoot production rates

(Epicormic Renewal Phase, Figure 3.11, c), or shoot production rates in both regular lateral branchlets and epicormic branchlets may decline (Decline 2 Phase, Figure 3.11, d). From the Epicormic Renewal Phase, epicormic branchlets may grow further to form new SCUs that become independent of the parent SCU (Figure 3.11, e). The parent SCU may then be classified as being in Decline 1 Phase if no other epicormic branchlets are present (Figure 3.11, f), remain in the Epicormic Renewal Phase if other epicormic branchlets are still expanding, or enter Decline 2 Phase if the remaining epicormic branchlets are declining (Figure 3.11, g).

Effects of epicormic shoot production on shoot and foliage dynamics

Ten percent to nearly 50% of shoots and foliage of branches are produced by epicormic shoots. Epicormic shoots produce a significant amount of shoots and foliage of mid- and lower-crown branches, suggesting that epicormic shoot production is an important process for maintenance of these branches. In all branches, higher percentages of current-year shoots and foliage are produced by epicormic shoots than for all shoots combined. In lower-crown branches, more than 50% of current-year shoots and foliage are produced by epicormic shoots. These results suggest that, in addition to maintaining shoot and foliage amount, epicormic shoot production leads to rejuvenation of shoots and foliage.

Upper-crown branches consist mainly of shoots and foliage on younger SCUs than do mid- and lower-crown branches. Differences among branches are most pronounced for the Tall Tree which has the deepest crown. This agrees with results of SCU development, and suggests that upper-crown branches are still growing while growth of mid- and lower-crown branches may be limited. Epicormic shoot production may be an important process for rejuvenating shoots and foliage and maintaining branch-level productivity in mid- and lower-crown branches.

The role of epicormic shoot production in crown maintenance

Epicormic shoot production is a constant process in crowns of old *P. menziesii* trees and leads to adaptive reiteration of SCUs. Ito (1996) found that growth rate and hydraulic conductance were higher for epicormic shoots compared with terminal shoots in crowns of *Quercus acutissima* Carruth., and suggests that epicormic shoot production may lead to renewal of shoots and foliage. As trees age, the balance between productive and non-productive organs becomes increasingly important in maintaining overall productivity of the tree crown (Remphrey and Davidson 1992, Sumida 1996). Epicormic shoot production works to generate productive organs from existing branching structure, resulting in efficient renewal of shoots and foliage. Kershaw et al. (1990) found that branch longevity ranged from 4 to 72 years in 10- to 130-year-old plantation-grown *P. menziesii*. I found branches with more than 100 annual rings, suggesting that branches may be maintained for longer periods in old *P. menziesii* trees. Epicormic shoot production may be an important mechanism for maintaining branch-level productivity and prolonging branch longevity in old *P. menziesii* trees.

In addition to adaptive reiteration of SCUs. I observed epicormic shoot production to occur at two larger scales in the crown of old *P. menziesii* trees (see Appendix). Epicormic shoot production from older sections of branches leads to formation of large sub-branch units. Sub-branch units that originated from epicormic shoots can be distinguished by their three-dimensional angle of attachment to the parent branching structure. Epicormic shoot production from the trunk and near the base of branches leads to formation of epicormic branches. Epicormic branches can be distinguished from original branches by a combination of distinguishing characteristics: smooth bark texture, tangent angle of attachment to the trunk, occurrence in multiple numbers within a small area of the trunk, and smaller diameter and shorter length relative to nearby original branches. All three lower-crown branches in this study were epicormic branches. Adaptive reiteration of SCUs. sub-branch units. and entire branches by epicormic shoot production may work to maintain the established crown of old *P. menziesii* trees after height growth and crown expansion have culminated, and contribute to prolonging individual tree life-span. making this species the "long-lived pioneer."

Table 3.1. General characteristics of sample branches.

Tree Branch position	Height (m)	Diameter (cm)	Length (m)	Age estimate (years)
Tall Tree				
DBH= 135.3 cm, H = 61.6 m				
Upper-crown	56.8	7.6	3.3	85
Mid-crown	35.4	20.0	8.1	162
Lower-crown	27.1	8.4	3.3	138
Medium Tree				
DBH= 153.5 cm, H = 58.7 m				
Upper-crown	50.8	8.6	4.3	79
Mid-crown	35.2	11.5	6.1	155
Lower-crown	21.2	5.3	2.8	70
Short Tree				
DBH= 93.9 cm, H = 50.8 m				
Upper-crown	45.9	6.0	3.1	105
Mid-crown	36.9	10.1	4.9	126
Lower-crown	26.8	7.8	2.4	75

Table 3.2. Frequency and timing of epicormic shoot production and their correlation with size, diameter, position and age of SCUs.

Tree Crown position	Total Number of SCUs	SCUs with epicormic branchlets (%)	Mean frequency (number/SCU)	r_s: **Frequency**				Mean timing (years)	r_s: **Timing**			
				Size†	Diameter	Position††	Age		Size†	Diameter	Position††	Age
Tall Tree												
Upper-crown	37	56.8	2.57a	0.499**	0.611**	-0.320	0.350*	6.72a	0.152	0.222	-0.294*	0.262
Mid-crown	116	89.7	5.45b	0.561**	0.668**	0.054	0.452**	6.25a	0.214**	0.078	-0.099	0.209**
Lower-crown	28	100.0	-	-	-	-	-	-	-	-	-	-
Medium Tree												
Upper-crown	42	81.4	4.97a	0.706**	0.611**	-0.197	0.394**	5.23a	0.205*	0.066	-0.222*	0.266**
Mid-crown	157	94.3	6.03a	0.510**	0.618**	-0.177*	0.429**	5.31a	0.160**	0.147**	-0.120**	0.234**
Lower-crown	54	94.4	5.90a	0.637**	0.674**	0.123	0.528**	5.08a	0.257**	0.196**	0.062	0.259**
Short Tree												
Upper-crown	19	73.7	5.50a	0.510*	0.835**	-0.321	0.289	5.59a	0.040	0.111	-0.111	0.106
Mid-crown	86	67.8	4.55a	0.675**	0.697**	-0.227*	0.336**	7.02b	0.211**	0.192**	0.104	0.315**
Lower-crown	27	82.1	8.36b	0.678**	0.611**	-0.093	0.734**	6.23a	-0.145	-0.151	-0.120	0.222**

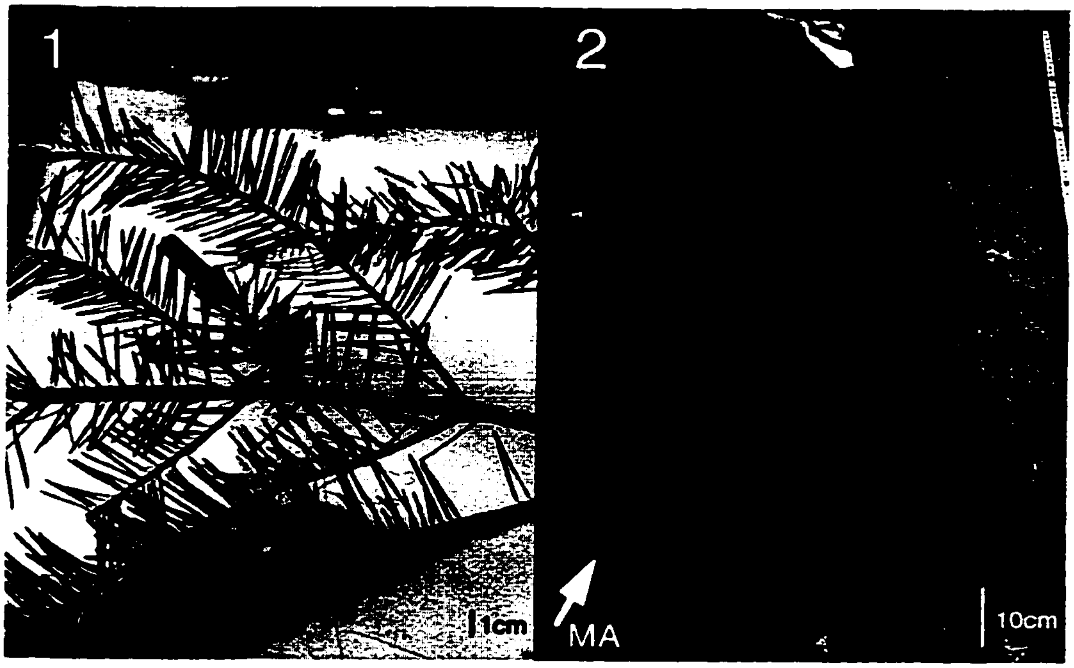
† length x width, †† distance from branch base.

Within the same tree, branch means labeled with the same letter are not significantly different (ANOVA and Tukey's HSD, $P > 0.05$).

r_s: Spearman's rank correlation coefficients: * $P < 0.05$, ** $P < 0.01$

Table 3.3. Total amount of shoots, foliage dry mass and foliage area of branches, and percentages produced by epicormic shoots. Number in parentheses represent amount and percentages of current-year shoots and foliage.

Tree Branch position	**Number of shoots**		**Foliage dry mass**		**Foliage area**	
	Total shoots	Epicormic (%)	Total (kg)	Epicormic (%)	Total (m^2)	Epicormic (%)
Tall Tree						
Upper-crown	3533 (1017)	9.9 (11.4)	1.000 (0.345)	7.0 (8.1)	4.235 (1.615)	8.0 (9.4)
Mid-crown	13577 (2108)	36.2 (50.4)	3.406 (0.625)	31.4 (54.2)	19.984 (4.599)	33.1 (46.6)
Lower-crown	3937 (714)	49.8 (66.0)	0.711 (0.109)	46.0 (64.6)	4.979 (0.988)	48.1 (64.9)
Medium Tree						
Upper-crown	6284 (1304)	23.3 (30.3)	1.332 (0.334)	19.7 (27.5)	6.984 (1.953)	20.1 (27.2)
Mid-crown	20178 (3228)	32.2 (44.1)	4.020 (0.750)	25.1 (37.0)	25.752 (5.639)	26.0 (37.2)
Lower-crown	6533 (1255)	40.9 (54.7)	0.827 (0.193)	34.4 (47.9)	6.586 (1.750)	34.3 (46.6)
Short Tree						
Upper-crown	2605 (583)	29.3 (35.6)	0.496 (0.119)	25.2 (32.4)	2.354 (0.727)	27.6 (34.6)
Mid-crown	12561 (1669)	19.7 (32.1)	2.316 (0.353)	16.6 (28.6)	13.892 (2.507)	17.4 (28.7)
Lower-crown	4112 (676)	38.6 (54.8)	0.584 (0.103)	33.0 (50.5)	3.942 (0.847)	33.7 (55.2)



Figures 3.1 - 3.2. Epicormic shoots (1) are produced from suppressed epicormic buds on older parent shoots, and can be distinguished by their internodal position on the parent shoot, vertical angle of attachment, and age difference. The shoot cluster unit (2) is an architectural unit of shoot organization in old *P. menziesii* trees consisting of a distinguishable main axis (MA), created by the extending terminal shoot, and several lateral branchlets. Regular lateral branchlets are produced by the original terminal bud that created the main axis, while epicormic branchlets (filled arrows) are produced when epicormic buds along the main axis are released from suppression. Shoots on SCUs were distinguished into "regular shoots" forming the main axis and regular lateral branchlets, and epicormic shoots forming epicormic branchlets. Many SCUs consist of both types of shoots.

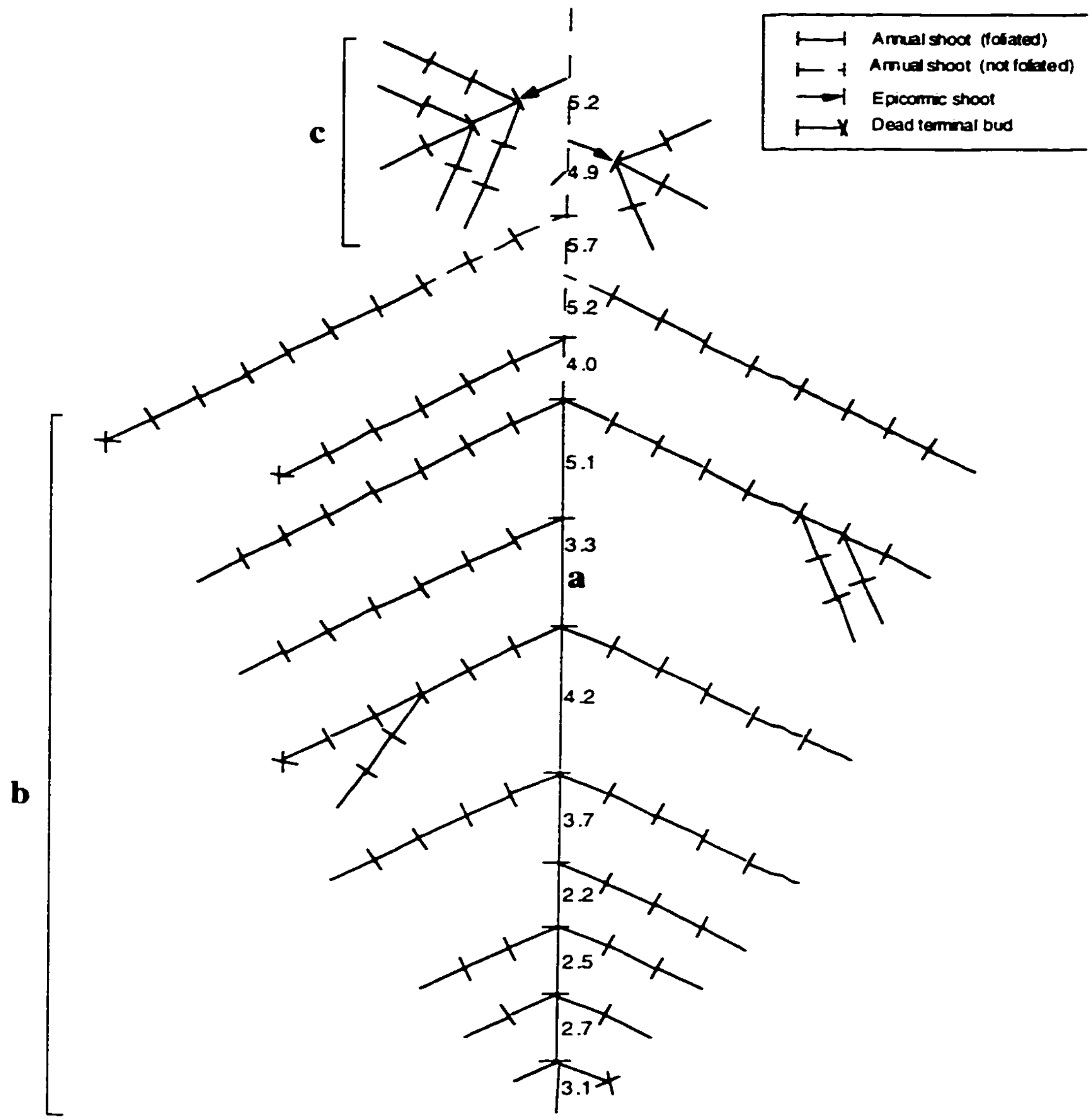


Figure 3.3. A map of the shoot cluster unit (SCU) showing the main axis (a), regular lateral branchlets (b) and epicormic branchlets (c). Numbers along the main axis denote the distance between branchlets (cm). Branchlets without a live terminal bud are marked with an X at the tip.

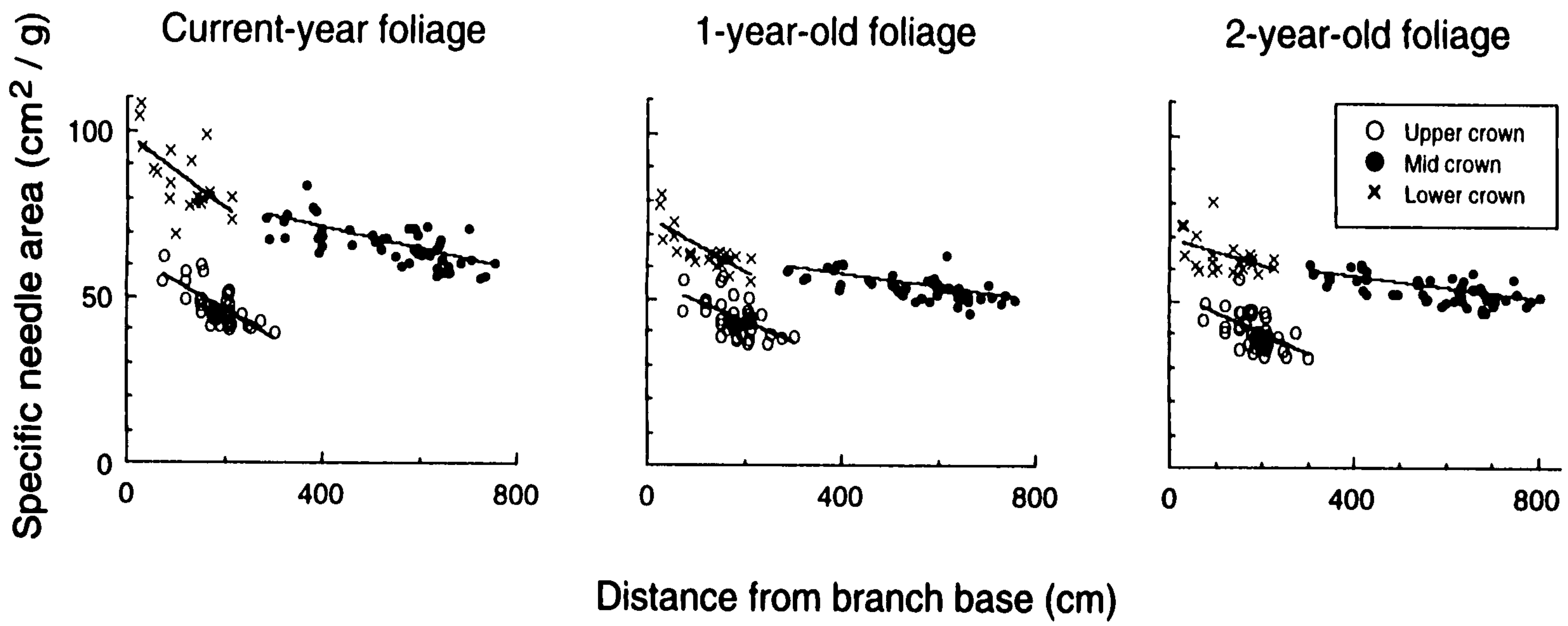


Figure 3.4. Examples of relationships between SCU position (distance from branch base) and specific needle area (SNA) of foliage-area samples. SNA for current-year, 1-year-old, and 2-year-old needles of regular shoots from upper crown (o), mid-crown (●), and lower-crown (x) branches of the Tall Tree are shown with linear-regression estimates of the relationship. These relationships were used to estimate SNA for SCUs where foliage-area samples were not taken. The measured and estimated SNAs were multiplied by foliage dry weight to obtain foliage area estimates for each shoot type and shoot age-class of SCUs.

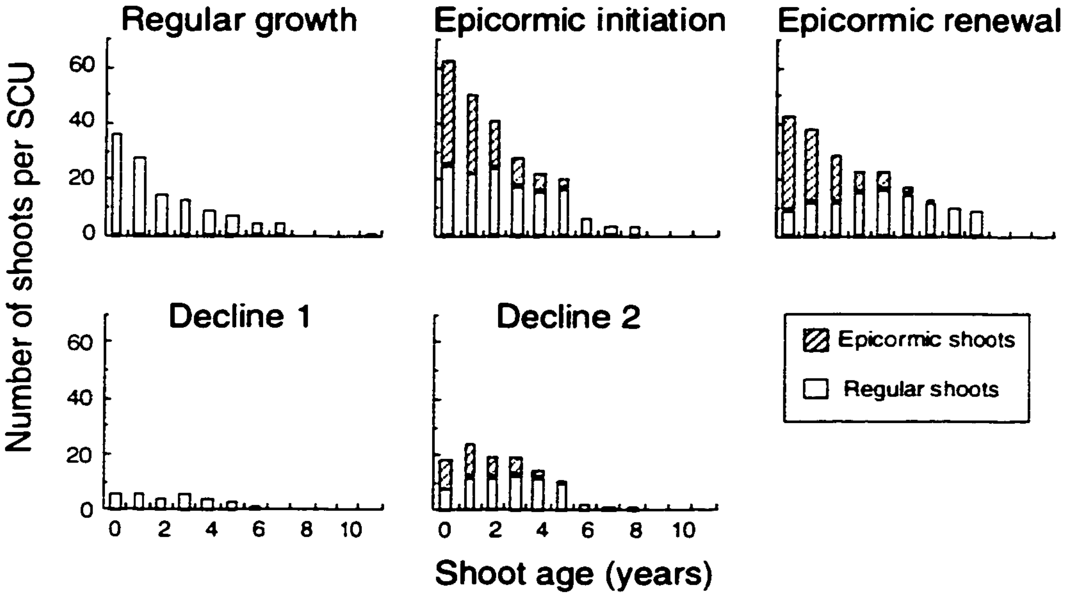


Figure 3.5. Examples of shoot age structures of SCUs from the mid-crown branch of the Tall Tree illustrating phases of SCU development. Each phase is characterized by shoot age structures of regular and epicormic shoots.

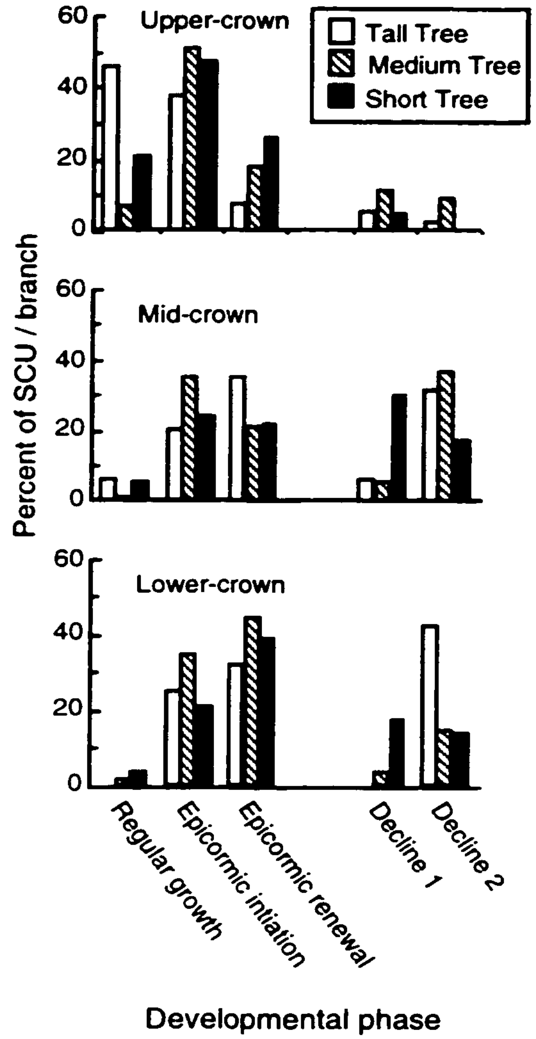


Figure 3.6. Percentages of SCU of each branch in the various phases of SCU development for the Tall Tree (open bars), Medium Tree (hatched bars), and Short Tree (filled bras).

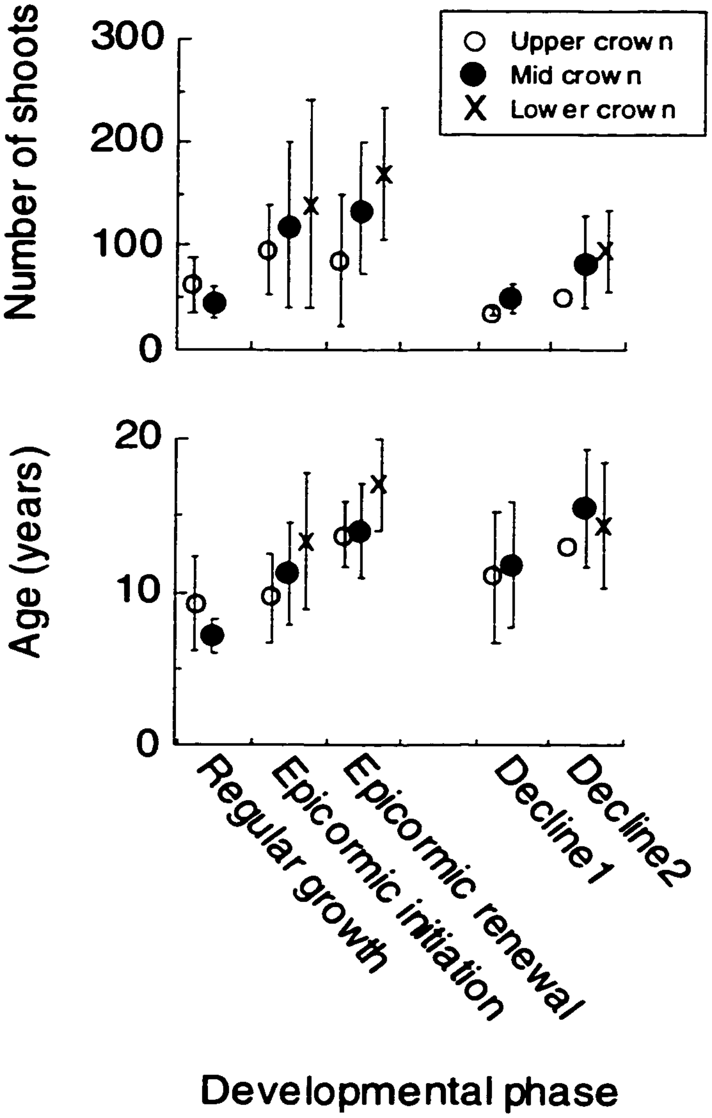


Figure 3.7. Mean number of shoots and mean age of SCUs in various phases of SCU development for upper-, mid- and lower-crown branches of the Tall Tree. Bars denote one standard deviation. No SCUs were observed in the Regular Growth Phase and Decline 1 Phase for the lower-crown branch.

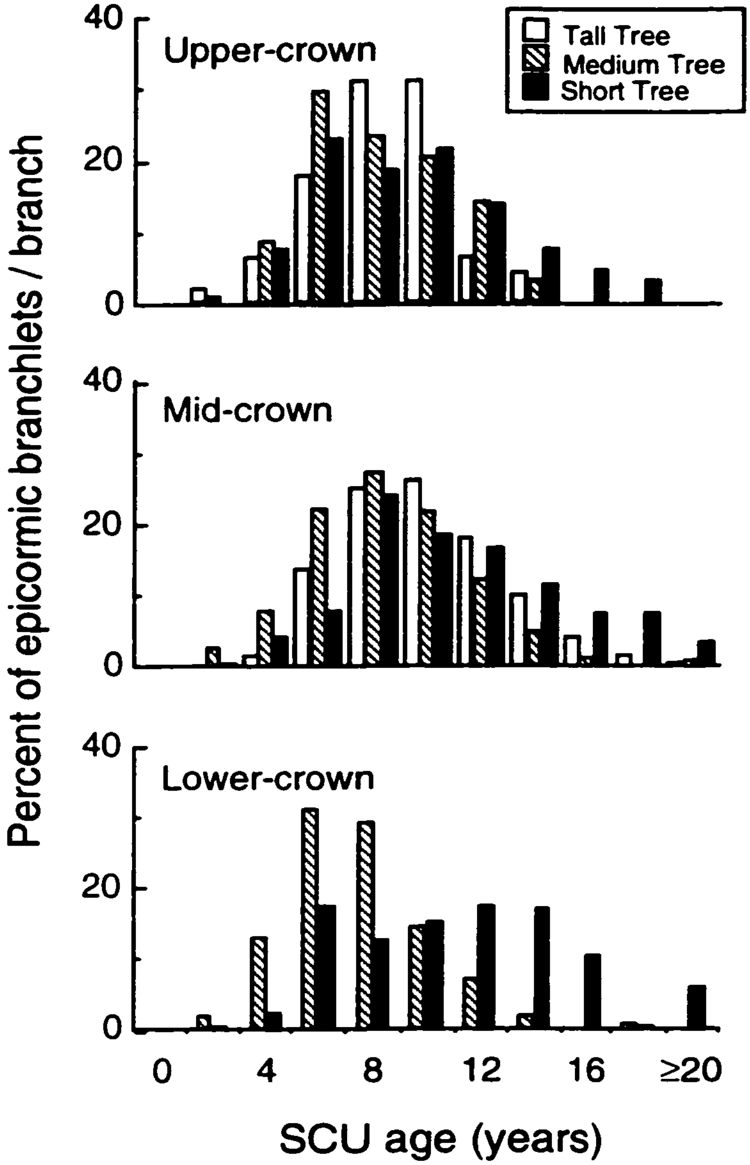


Figure 3.8. Frequency distributions of SCU age when epicormic branchlets were produced, calculated by subtracting the age of each epicormic branchlet from the SCU age. SCU ages are shown in two-year age-classes.

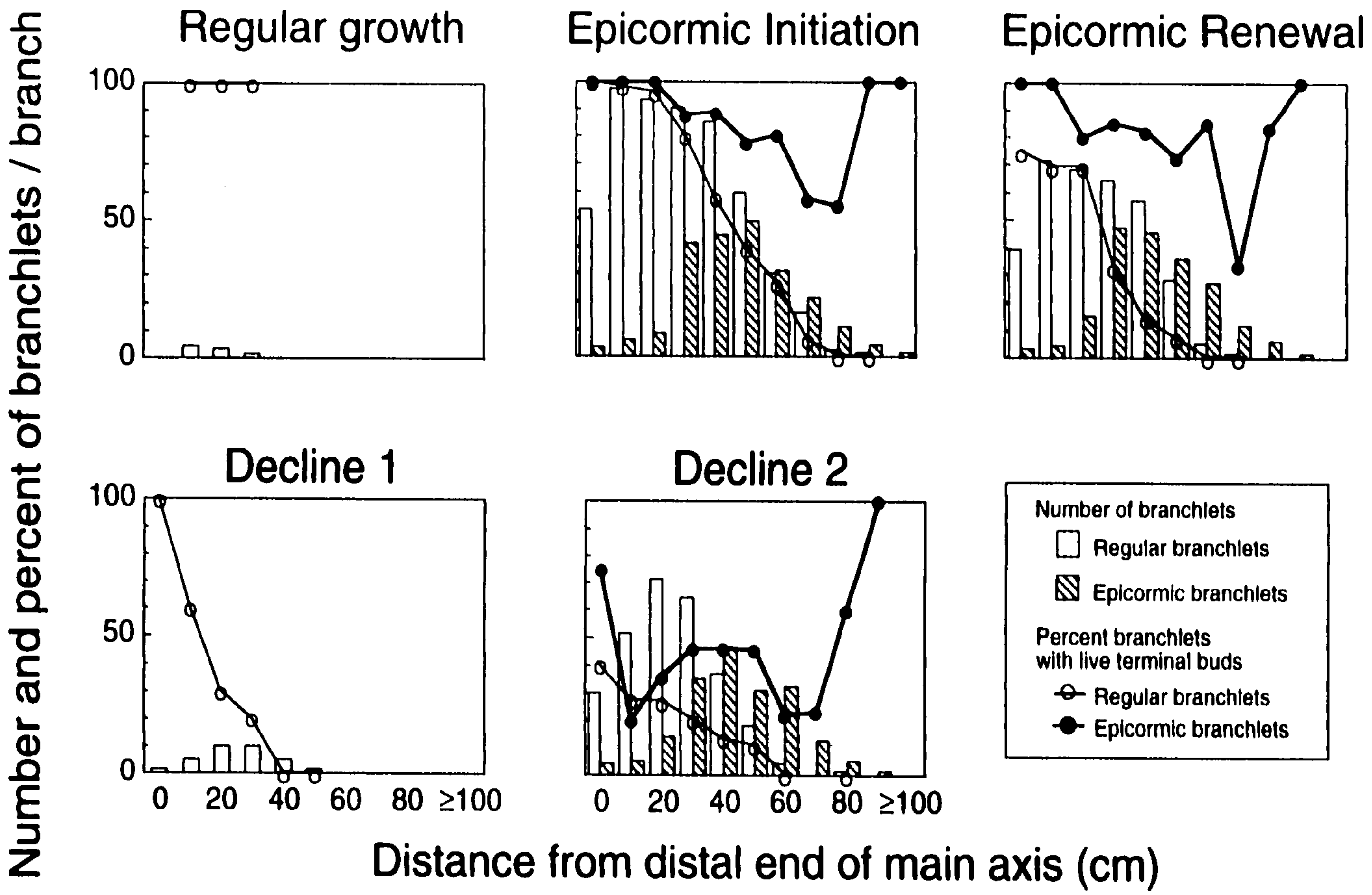


Figure 3.9. Morphological characteristics of SCUs in various phases of SCU development for the mid-crown branch of the Medium Tree. Bars show frequency distributions regular lateral branchlets (open bars) and epicormic branchlets (hatched bars) along main axes of SCUs in 10cm distance classes. Lines show percentages of regular (open circles) and epicormic branchlets (filled circles) in each distance class that have live terminal buds.

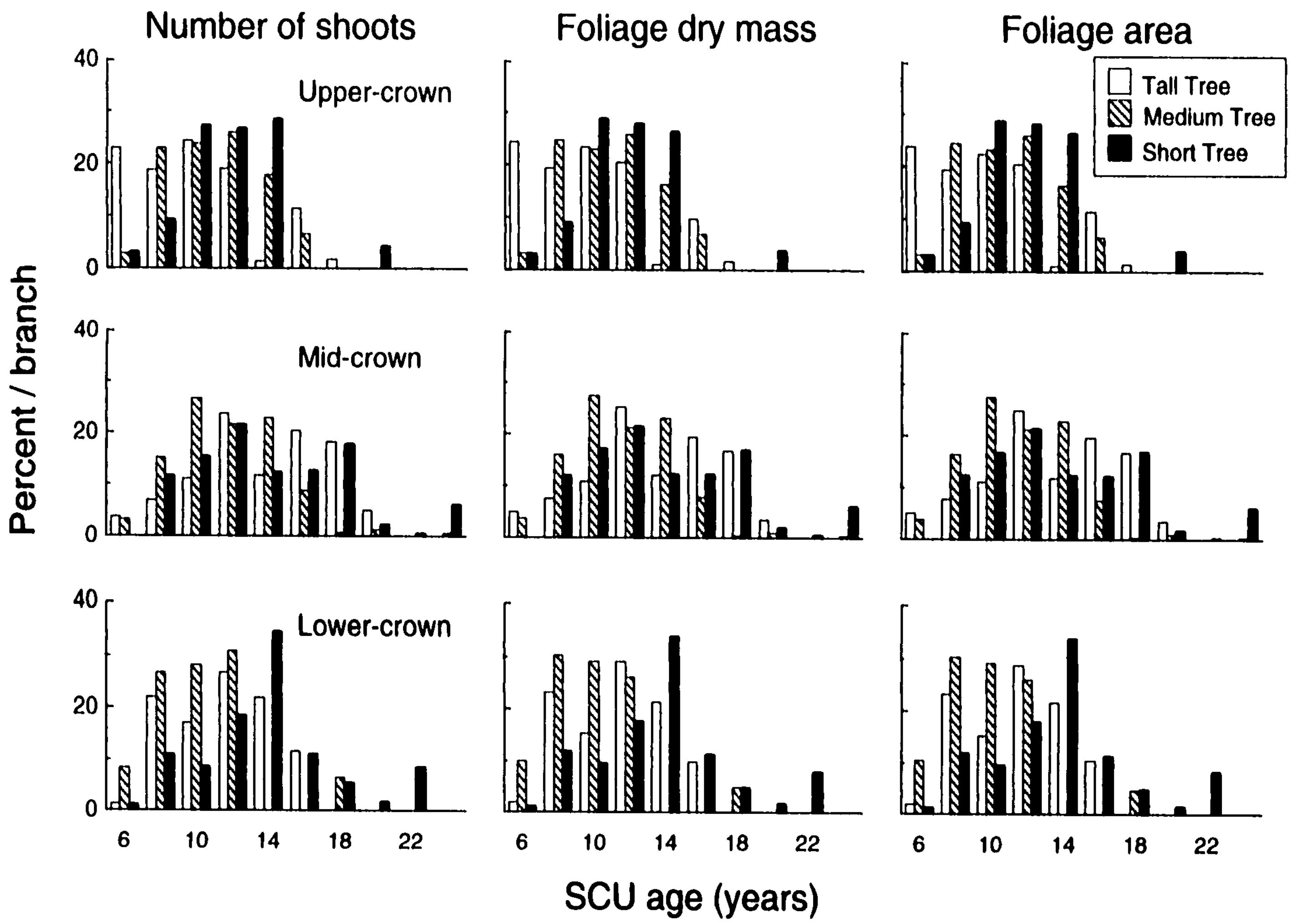


Figure 3.10. Percentages of shoots, foliage dry weight, and foliage area in each branch born on SCUs of various ages. SCU ages are shown in 2-year age-classes.

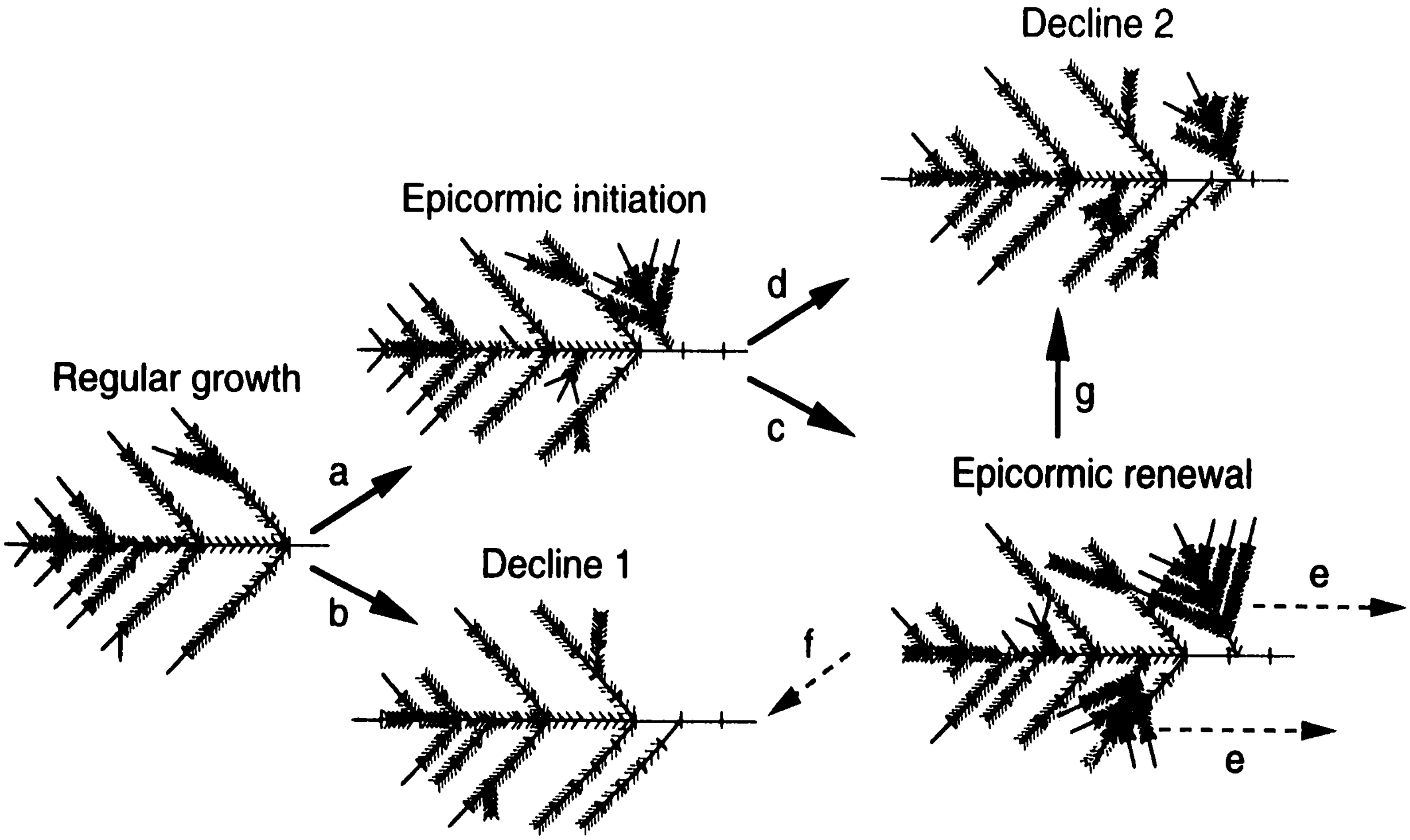


Figure 3.11. Schematic diagram showing the branching pattern and developmental phases of SCUs. Light-colored foliage denotes current-year shoots, while dark-colored foliage denotes older shoots. Arrows (a - g) denote transitions between phases for the entire SCU (solid lines) and parts of SCUs (dotted lines).

CHAPTER IV

Architectural characteristics of old-growth *Pseudotsuga menziesii* and implications for understanding ecological significance of tree architecture

Introduction

Growth and morphology of trees have been associated with their successional status (Horn 1971, Bazzaz 1979, Schultze 1982, Givnish 1988, Küppers 1989, King 1998). Early successional species generally have: higher growth rate and smaller maximum size, indeterminate shoot growth and greater bifurcation ratio, more foliage overlap and shorter foliage life-span, than late-successional species (Millet et al. 1998, Table 4.1). These characteristics are presumed to be adaptive responses to environmental conditions experienced by early- and late-successional species during respective stages of succession (Bazzaz and Carlson 1982). However, Millet et al. (1998) point out the limitations of such static views of tree architecture and propose that a more dynamic approach is needed to link individual-based traits to community-level dynamics.

Millet et al. (1998) argue that, because architectural characteristics of trees change during their development, a static conception of tree architecture cannot be attributed to species. For example, Whitney (1976) proposed that bifurcation ratio was a species-specific characteristic that reflected the successional status of species, with early-successional species having higher bifurcation ratios than late-successional species. However, this theory has been refuted by studies that found bifurcation ratios to be variable among trees of the same species (Borchert and Slade 1981, Steingraeber 1982). Plasticity within species has been found for various other architectural characteristics (e.g. Fisher and Hibbs 1982, Canham 1988), casting doubt on the static conception of tree architecture as related to species' successional status. Millet et al. (1998) propose that dynamics of tree architecture need to be considered in understanding the adaptive significance of architectural characteristics. They raise dynamics such as, potential for vegetative reproduction, potential to survive under suppressed growth form, and potential to recover damaged axes, and argue that survival of a species in a community depends on its "potentialities", i.e. degree of plasticity of architectural characteristics.

Pseudotsuga menziesii is a pioneer species in mid-elevation coniferous forests of the Pacific Northwest Coast of North America. However, this species is also very long-lived and coexists for centuries with late-successional species in old-growth forest. Franklin et al. (1981) used the term 'long-lived pioneer' to describe the role of *P. menziesii* in community dynamics of *Pseudotsuga-Tsuga* forests. Persistence of *P. menziesii* results in long-term coexistence with late-successional species. In previous chapters, I elucidated four canopy processes that contribute to long-term coexistence of *P. menziesii* with late-successional species and to long-term survival of individual trees of *P. menziesii*. Canopy processes that contribute to long-term coexistence are:

(1) Vertical stratification: Old-growth *P. menziesii* dominates in the upper canopy, above the crowns of more shade-tolerant, late-successional

species. Measurement and projection of current height-growth rates indicate that this dominance will continue for at least another century (Chapter 1).

(2) Decreasing crown competition in the upper canopy: Height growth and crown expansion culminate in large trees of all species, indicating that crown competition decreases with increasing tree size. This allows large trees of different species that survive the initial competitive exclusion stage to coexist in the upper canopy (Chapter 2).

Canopy processes that contribute to long-term survival are:

(3) Morphological acclimation: Old-growth *P. menziesii* have deep crowns with low branch density, and symmetric branching pattern that result in efficient shoot and foliage display. Marked differences between crown form and branching pattern in comparison to young and mature trees reflects high degrees of morphological plasticity and acclimation to late-successional conditions (Chapter 2).

(4) Crown maintenance: Epicormic shoot production in old-growth *P. menziesii* results in adaptive reiteration of shoot cluster units, sub-branch units, and entire branches. This may be an important mechanism for maintaining productivity of the established crown after height growth and crown expansion have culminated, and contribute to prolonging individual tree life-span (Chapter 3).

Results from previous chapters indicate that characteristics associated with early-successional species, such as high growth rate, low maximum height, indeterminate shoot growth, high bifurcation ratio, and short lifespan do not apply to old-growth *P. menziesii*. Long-lived species such as *P. menziesii* illustrate how architectural characteristics of trees can change during their development, and the need for a more dynamic and holistic view relating tree architecture to community dynamics to understand the ecological significance of architectural characteristics of species. In this chapter, I review the architectural characteristics of *P. menziesii* in light of the dynamic approach to tree architecture as proposed by Millet et al. (1998), and discuss how they contribute to persistence of *P. menziesii* in old-growth *Pseudotsuga-Tsuga* forest. I also discuss the ecological significance of these characteristics and their effects on community and ecosystem dynamics of old-growth *Pseudotsuga-Tsuga* forests.

Vertical stratification

Conventional models of forest succession predict that early-successional species have high growth rate and low maximum height, and are eventually shaded out by more shade-tolerant, late-successional species (Bazzaz 1979). However, old-growth *P. menziesii* have low height-growth rate, and maximum attainable height similar to or greater than coexisting late-successional species (Ishii et al. 2000), and these characteristics may contribute to its function in the community as a long-lived pioneer.

P. menziesii dominates in the upper-most part of the forest canopy at Wind River, comprising nearly 70% of trees above 50m in height. As shown through analyses and projection of height-growth rates in Chapter 1, there are no differences in maximum attainable height among *P. menziesii*, *T. heterophylla*, and *T. plicata*. *A. amabilis* was distinguished as having lower maximum attainable height than these three species, making it a mid- to lower-canopy species in this forest. Although maximum attainable height for *T. brevifolia* could not be accurately determined due to very large uncertainty, observations suggest that it is a lower-canopy species. Current height-growth rates indicate that *P. menziesii* will continue to dominate in the upper canopy for at least another century.

P. menziesii dominates in the upper canopy of mixed-species second-growth stands in early stages of succession (Wierman and Oliver 1979, Larson 1986). Studies of stand structure in old-growth forests, ranging in age from 400 to 800 years old, have found that *P. menziesii* continue to dominate in the upper canopy for centuries into later stages of succession (Gholz et al. 1976, Stewart 1986b, Spies et al. 1990, Easter and Spies 1994). These observations suggest that dominance of *P. menziesii* in the upper canopy of old-growth *Pseudotsuga-Tsuga* forests is largely the result of differences among species in their timing of establishment, and can last for centuries. Prolonged dominance of *P. menziesii* in the upper canopy and the resulting vertical stratification may contribute to long-term coexistence of relatively shade-intolerant *P. menziesii* with late-successional species in old-growth *Pseudotsuga-Tsuga* forests.

Decreasing crown competition in the upper canopy

Competition among species for a single resource, such as light, often results in exclusion of species (Tilman 1988). Conventional models of succession predict that early-successional species are eventually out-competed by late-successional species. However, competing species can coexist if resource availability oscillates, or is spatially variable and the effects of competition are localized (Shmida and Ellner 1984, Tilman 1988). As shown in Chapter 2, large trees of various species may coexist in the upper canopy of this forest because crown competition among large trees is low. Crown expansion rate decreases for all species as tree size increases, indicating that competition for crown space decreases with increasing tree size. Crown expansion rates are low throughout the entire crown for large trees of all species, including the entire *P. menziesii* population. In contrast, crown expansion rates for small trees, including individuals of shade-tolerant *A. amabilis*, *A. grandis* and *T. heterophylla*, are high in the upper crown and decrease toward the lower crown despite small changes in local light environment. These results indicate that while crown competition among large trees is low, competition among small trees is intense, and crown expansion into high-light areas of the upper canopy is important for the small trees. Decreasing crown competition with increasing tree size may allow large trees of different species that survive the initial competitive exclusion stage to coexist in the upper canopy of this forest.

Morphological acclimation

Indeterminate shoot growth and high bifurcation ratio are some morphological characteristics generally associated with early-successional tree species. However, as shown in Chapter 2, old-growth *P. menziesii* has determinate shoot growth, and has lower bifurcation ratio than late-successional *A. amabilis*, *A. grandis*, and *T. heterophylla*. Comparison of morphological characteristics of old-growth *P. menziesii* with published studies on young and mature trees (less than 100 years old) suggests that morphological characteristics of *P. menziesii* change during development. Young and mature *P. menziesii* trees grown in plantations have dense crowns with numerous internodal branches (Jensen and Long 1983) resulting in high branch density. Branch densities as high as 8 - 21 branches per vertical meter of trunk have been reported for 10- to 20-year-old trees (Maguire et al. 1994, St. Clair 1994, Kershaw and Maguire 1995), 2 to 4 times that of old-growth trees in this study. Bifurcation ratios are also much higher for young and mature *P. menziesii* trees, ranging from 1.3 to as high as 5.3 for 10- to 50-year-old trees (Owens 1969, Mitchell 1974), while maximum bifurcation ratios found for old-growth trees in this study are 1.4 to 1.7.

These marked differences in crown form and branching pattern of old-growth *P. menziesii* compared with young and mature trees may be the result of physiological limitations on growth due to increasing age, size and complexity. As discussed by Ryan and Yoder (1997), these differences may be the result of age and size related physiological limitations on tree growth, such as increases in respiratory tissue, nutrient limitation, genetic changes in meristematic tissue, and hydraulic limitation. Marked changes in crown form and branching pattern in old-growth *P. menziesii* also reflect high degrees of morphological plasticity in this species. Sparsely branched crowns and symmetrical branching pattern results in efficient display of foliage area, and may be viewed as morphological acclimation to late-successional conditions.

Crown maintenance

According to conventional models of forest succession, early-successional species are generally short-lived and this characteristic contributes to their eventual replacement by long-lived, late-successional species. However, *P. menziesii* is also an exception to this rule, as individual trees can live over 1000 years, nearly twice as long as some shade-tolerant species, and persist in the forest for centuries (Franklin and Hemstrom 1981). In their population dynamics study of the same stand as this study, Franklin and DeBell (1988) predict that, if current mortality rates continue, *P. menziesii* would persist in the forest for an additional 755 years.

In Chapter 3, I showed that shoots and foliage on branches of old *P. menziesii* trees are constantly renewed by epicormic shoot production. Epicormic shoots are produced in all parts of the crown, and epicormic buds remain dormant for 5-6 years on average. Epicormic shoot production results in adaptive reiteration of shoot cluster units (SCUs), an architectural unit of shoot organization within branches. Five phases of SCU development were identified based on relative age-structures of regular and epicormic shoots. SCUs produce epicormic branchlets as early as 3-4 years in age, and peak production occurred around 7-12 years. Epicormic branchlets occur toward the proximal end of main axes of SCUs where regular lateral branchlets are no longer producing new shoots. In some lower-crown branches, nearly 50% of shoots and foliage are epicormic shoots. Demographic analysis of SCUs showed that upper-crown branches are still growing in size, while mid- and lower-crown branches have reached maximum size, and are being maintained by adaptive reiteration of

SCUs. In addition to adaptive reiteration of SCUs, epicormic shoot production occurs at two larger scales in old *P. menziesii* trees. Epicormic shoot production from older parts of branches leads to reiteration of large sub-branch units. Epicormic shoot production from the trunk and near bases of branches leads to formation of epicormic branches. (See Appendix for detailed analysis of adaptive reiteration at the sub-branch and branch scales.)

As trees age, the balance between productive and non-productive organs becomes increasingly important in maintaining overall productivity of the tree crown (Remphrey and Davidson 1992, Sumida 1996). Epicormic shoot production generates productive organs from existing branching structure, resulting in efficient renewal of shoots and foliage. The observations presented here indicate that epicormic shoot production in the crown of old *P. menziesii* trees is a constant process that occurs without exogenous stimuli, such as damage or changes in light environment. Epicormic shoot production from foliated shoots, from older sections of branches, and from the trunk and bases of branches, results in adaptive reiteration of new SCUs, sub-branch units, and entire branches, respectively. Adaptive reiteration of various architectural units by epicormic shoot production is an important mechanism for maintaining productivity of the established crown of old *P. menziesii* trees after height growth and crown expansion have culminated, and contribute to prolonging individual tree longevity. This may be an important process contributing to persistence of *P. menziesii* in old-growth *Pseudotsuga-Tsuga* forests.

Discussion

Ecological significance of architectural characteristics contributing to persistence of P. menziesii

This study elucidated four canopy processes that contribute to persistence of *P. menziesii* in old-growth *Pseudotsuga-Tsuga* forest. Vertical stratification among coexisting tree species and decreasing crown competition in the upper canopy contribute to long-term coexistence of *P. menziesii* with late successional species. Morphological plasticity resulting in acclimation to late-successional conditions and crown maintenance by epicormic shoot production contribute to long-term survival of individual trees of *P. menziesii*. Although old-growth *P. menziesii* shows some characteristics of early-successional species such as higher photosynthetic rate, higher respiration rate (S.C. Thomas and W.E. Winner, in preparation), and shorter foliage lifespan (H. Ishii and E.D. Ford, unpublished data) relative to coexisting late-successional species, previous chapters have shown that several characteristics of old-growth *P. menziesii*, such as low growth rate, high maximum height, determinate shoot growth, low bifurcation ratio, and long lifespan, do not conform to general characteristics of early-successional species. In addition, marked differences between architectural characteristics of old-growth *P. menziesii* in comparison to young and mature trees, implies high degrees of morphological plasticity in this species. Because architectural characteristics of species may be influenced by factors other than the immediate environment of the individual, various aspects of the species' ecology as well as its role in community dynamics need to be considered to understand the ecological significance of tree architecture.

Community dynamics of *Pseudotsuga-Tsuga* forests of the Pacific Northwest Coast of North America do not conform to conventional models of forest succession (Figure 4.1). Under the equilibrium model of succession (Clements 1916, Gleason 1926, Odum 1971, Pickett 1976), early-successional species are gradually replaced by late-successional species resulting in late-successional steady state or equilibrium community (Figure 4.1A). This model was later modified to the non-equilibrium model of succession (e.g. Loucks 1970, Bormann and Likens 1979, reviewed by Shugart and West 1981 and, Sprugel 1991), where return intervals for stand-replacing disturbance is shorter than the time period required for late-successional steady state to occur (Figure 4.1B). Sprugel (1991) points out that if the spatial scale of stand-replacing disturbance is sufficiently large, an equilibrium community may never be reached. However, the current species composition of *Pseudotsuga-Tsuga* forests of the Pacific Northwest Coast of North America cannot be explained by either of these models. *P. menziesii*, the pioneer species, is extremely long-lived, and has persisted in the forest for centuries resulting in long-term coexistence with late-successional species. This dynamic may be regarded as the 'extended non-equilibrium' model of succession where return intervals for stand-replacing disturbance are long, and pioneer species are long-lived, resulting in long-term coexistence with late-successional species between infrequent disturbances (Figure 4.1C).

In the case of *P. menziesii*, characteristics associated with long-term coexistence and survival may be linked with the extended non-equilibrium community dynamic. In the Pacific northwestern coast of North America, *P.*

menziesii depends on large-scale, low-frequency disturbances, such as stand-replacing fires for extensive regeneration (Spies and Franklin 1989, Stewart 1989). Return intervals for stand-replacing fires in this region can be 500 years or more (Agee 1991). Between such fires, *P. menziesii* regeneration in the understory is very limited (Franklin and Dyrness 1973). So, it is critical that mature individuals survive for centuries from one disturbance event to the next. In addition, *P. menziesii* trees are known to survive several small fires during their lifetime (Agee 1993). Expression of characteristics associated with long-term coexistence and survival may be linked with the fire-dependent regeneration and fire-surviving characteristics of this species. This example illustrates that, in addition to the immediate environment of the individual, modes of reproduction and long-term dynamics of the species in the community need to also be considered to understand the ecological significance of architectural characteristics (Millet et al. 1998), especially for long-lived species such as *P. menziesii*.

Directions for future research

The findings and theory presented here represent a comprehensive view of the adaptive significance of architectural characteristics in long-lived trees, as well as their role in forest succession. The persistence of long-lived pioneers such as *P. menziesii*, and the resulting community dynamics of *Pseudotsuga-Tsuga* forests do not conform to conventional theories of forest succession, suggesting that these theories are not universally applicable, and that a more holistic view is necessary in order to understand forest succession and species' adaptation. Further research in other forest ecosystems characterized by long-lived species, e.g., *Sequoiadendron giganteum, Seqouia semprevirens, Thuja plicata,* may lead to a better understanding of the long-term dynamics of forests and formation of a more comprehensive theory of forest succession. In addition, evolution of longevity is an interesting question. I have elucidated several characteristics that may contribute to longevity of *P. menziesii*. Further research on whether these characteristics are shared among other long-lived trees, may provide more insight into the evolution of longevity.

I have shown that conventional interpretations of tree architecture as a static characteristic corresponding to successional status of species may need to be reconsidered. In addition to *P. menziesii*, late-successional *T. heterophylla*, another major component of old-growth *Pseudotsuga-Tsuga* forests has many characteristics conventionally associated with early-successional species: small numerous needles, indeterminate shoot growth, and short life-span. Development of a more comprehensive and dynamic understanding of tree architecture may be needed to interpret the interaction between these two dominant species of *Pseudotsuga-Tsuga* forests.

Table 4.1 Characteristics of early- vs. late-successional species.

Characteristic	**Early successional species**	**Late successional species**
Physiology	high photosynthetic rate	low photosynthetic rate
	high respiration rate	low respiration rate
Leaves	small	large
	numerous	few
	random orientation	planar orientation
	overlapping	limited overlap
	fast turnover	slow turnover
Shoots	indeterminate growth	determinate
	long growing season	short growing season
Branching	high bifurcation ratio	low bifurcation ratio
Growth	rapid growth	slow growth
	high biomass production	low biomass production
	height growth favored	lateral growth favored
	low maximum height	high maximum height
	short lifespan	long lifespan

Based on Millet et al. (1998) Table 2.

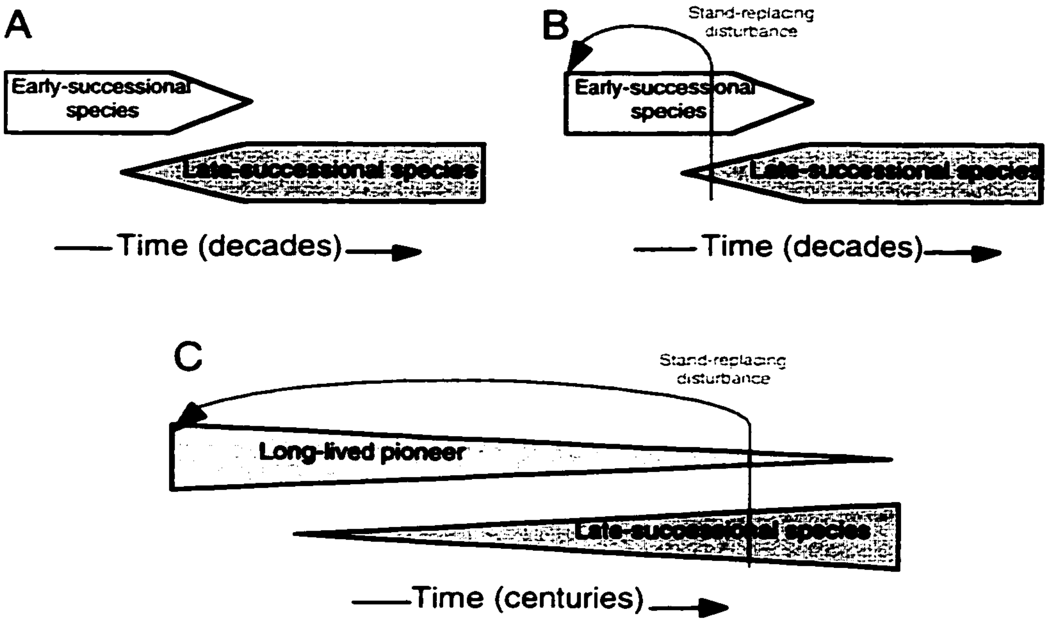


Figure 4.1 Schematic diagram representing various models of forest succession. Bar width represents relative abundance of species. Under the equilibrium model (A), early-successional species are gradually replaced by late-successional species resulting in late-successional steady state. Under the non-equilibrium model (B) return intervals for stand-replacing disturbance are shorter than the time period required for late-successional steady state to occur. Under the extended non-equilibrium model (C), return intervals for stand-replacing disturbance are long, and long-lived pioneer species persist, resulting in long-term coexistence with late-successional species between infrequent disturbances.

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APPENDIX

Adaptive reiteration of sub-branch units and branches by epicormic shoot production

In Chapter 3, I showed that shoots and foliage on branches of old-growth *P. menziesii* are maintained by epicormic shoot production and proposed that this process may contribute to this species' longevity. Adaptive reiteration by epicormic shoot production occurs at three different scales in old-growth *P. menziesii*, and together they work to maintain the established crown. Epicormic shoot production from foliated shoots results in adaptive reiteration of shoot cluster units (SCUs). Epicormic shoot production from older parts of branches leads to reiteration of large sub-branch units. Epicormic shoot production from the trunk and near bases of branches leads to formation of epicormic branches. Adaptive reiteration of SCUs was described in Chapter 3. Here I describe in detail reiteration processes of sub-branch units and epicormic branches

Sub-branch units that originate from epicormic shoots can be distinguished by their three-dimensional angle of attachment to the parent branching structure that results from the vertical angle of attachment of the epicormic shoot to the parent branch section (Figure A.1A). If we consider the original terminal bud that grew out of the trunk as the initial 'generation', and epicormic buds as subsequent 'generations', a single branch can consist of successive generations of sub-branch units produced by repeated epicormic shoot production (Figure A.1B). The extent of development of generations of sub-branches increases with increasing branch size and age (Figure A.2). Mid-crown branches are larger and older than upper- and lower-crown branches, and consist of up to 6 to 7 generations of sub-branches. Upper- and lower-crown branches consist of up to 4 to 5 generations of sub-branches. The percentage of current-year shoots in each generation increases with increasing generation in all branches except the upper-crown branch of the Tall Tree. This indicates that the production rate of new shoots is higher in younger generations of sub-branches, and suggests that reiteration of sub-branch units through epicormic shoot production promotes foliage rejuvenation. The average production rate of new generations of sub-branches (R_g) was estimated by dividing branch age by total number of generations in each branch. These rates range from once every 15.0 - 27.6 years with a mean of 19.5 years. As another method for estimating production rate of new generations of sub-branches, cross-sections were taken from the parent and epicormic branch sections of several three-dimensional forks and annual rings on each section were counted to calculate their age difference (Table A.1). These estimates range from 5 to 58 years with a mean of 23.5 years. These estimates are approximate, as error may result from missing rings (Reukema 1959, Kershaw et al. 1990). Nevertheless they suggest that, on average, epicormic shoot production leading to the formation of new sub-branch units occurs approximately every 20 years. Kershaw et al. (1990) found that branch longevity ranged from 4 to 72 years in 10- to 130-year-old, plantation-grown *P. menziesii*. In this study, branches with more than 100 annual rings were found, suggesting that branches may be maintained for longer periods in old-growth *P. menziesii* trees. Reiteration of sub-branch units by epicormic shoot production may be an important mechanism for prolonging branch longevity in old *P. menziesii* trees.

While original branches are produced by the terminal bud of the tree, epicormic branches are produced from dormant buds on the trunk or at bases of branches (Zimmermann and Brown 1971, Bryan and Lanner 1981). Based on observations of epicormic branches at various stages of development, the following criteria were developed for distinguishing epicormic branches from original branches (Figure A.3):

(1) Bark texture: Because of their younger age relative to the trunk, the bark of epicormic branches is often smooth and light grey colored, similar to the trunk of young *P. menziesii* trees. Original branches are as old as the part of the trunk they are attached to, and have rough, dark brown bark. Epicormic branches can be distinguished by the difference in bark texture relative to the trunk.

(2) Angle of insertion: Epicormic branches often grow out of the trunk at tangent angles, due to their origin in the axils of branches or near the base of the branch. Original branches originate in the pith of the trunk and grow out at right angles to the trunk. Epicormic branches can be distinguished by their tangent angle of insertion to the trunk.

(3) Associated dead or declining branch: Several epicormic branches can grow out near the base of a dead or dying branch, perhaps due to some stimulus from the older declining branch that triggers release of several epicormic buds from near its base. Epicormic branches can be

distinguished by presence of an associated older branch that is dead or declining.

(4) Fan-shaped branch clusters: Several epicormic branches can grow out from the same area of the trunk. These may thin out and leave behind three to four branches that are arranged in a fan-shaped cluster. Epicormic branches originating from such clusters can be distinguished by their fan-shaped arrangement.

(5) Callus-like swell: The growth of several epicormic branches from the same area of the trunk can result in a callus-like swell at the base of the branches. The swell may persist after many of the epicormic branches thin out. The remaining epicormic branches can be distinguished by presence of this callus-like swell that can be distinguished from the smooth taper observed at the branch collar of original branches.

(6) Smaller relative diameter: Diameter of epicormic branches is often smaller relative to nearby original branches because of their younger age. Although suppressed original branches can also have small diameter, branch diameter can be used in conjunction with other characteristics above to distinguish epicormic branches.

By combining these criteria, branches of seven old-growth *P. menziesii* trees were distinguished as being 'original' or 'epicormic' (Figure A.4). Epicormic branches comprise between 14.6% and 83.3% of live branches in these trees, and form an 'inner crown' inside the outer crown formed by original branches. The extent of development of the inner crown varies from tree to tree and may reflect stages of crown development associated with the growth history of each tree. The oldest original branches are found in the mid-crown, and the lower crown consists almost entirely of epicormic branches. Although silvicultural studies have concluded that epicormic branching is not a common phenomenon in young and mature *P. menziesii* (Reukema 1959), it may be an important process for crown maintenance in old trees.

As trees age, the balance between productive and non-productive organs becomes increasingly important in maintaining overall productivity of the tree crown (Remphrey and Davidson 1992, Sumida 1996). Epicormic shoot production generates productive organs from existing branching structure, resulting in efficient renewal of shoots and foliage. The observations presented here indicate that epicormic shoot production in the crown of old-growth *P. menziesii* is a constant process that occurs without exogenous stimuli, such as damage or changes in light environment. Epicormic shoot production from foliated shoots, from older sections of branches, and from the trunk and bases of branches, results in adaptive reiteration of new SCUs, sub-branch units, and entire branches, respectively. Adaptive reiteration of various architectural units by epicormic shoot production may be an important mechanism for maintaining productivity of the established crown of old *P. menziesii* trees after height growth and crown expansion have culminated, and contribute to prolonging individual tree longevity. This may be an important process contributing to persistence of *P. menziesii* and its long-term survival in old-growth *Pseudotsuga-Tsuga* forests.

Table A.1. Ages and age differences of the parent and epicormic cross sections of three-dimensional forks within branches where sub-branch units were produced by epicormic shoot production. Sample trees and branches are the same as in Chapter 3.

Tree Crown-level	Parent age	Epicormic age	Age difference
Tall Tree			
Upper	78	32	46
Mid	46	37	9
	94	69	25
Lower	no samples taken		
Medium Tree			
Upper	27	15	12
	17	12	5
Mid	70	12	58
	104	67	37
Lower	48	23	25
	44	35	9
Short Tree			
Upper	88	58	30
	23	13	10
Mid	58	34	24
	44	28	16
Lower	no samples taken		

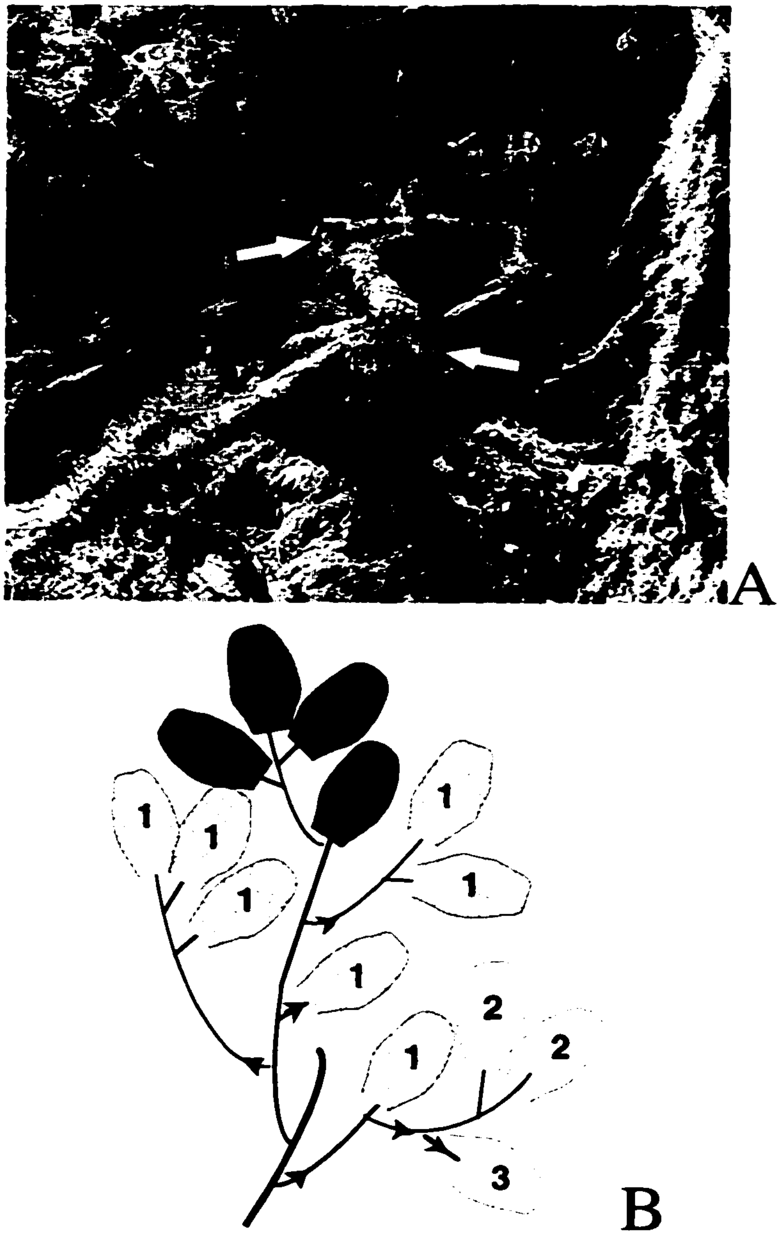

Figure A.1 Three-dimensional forks (A, white arrows) within branches where sub-branch units were produced by epicormic shoot production. As a result of the successive production of sub-branch units by epicormic shoot production (B, black arrows), foliage on different parts of the branch originate from different “bud generations” (numbers).

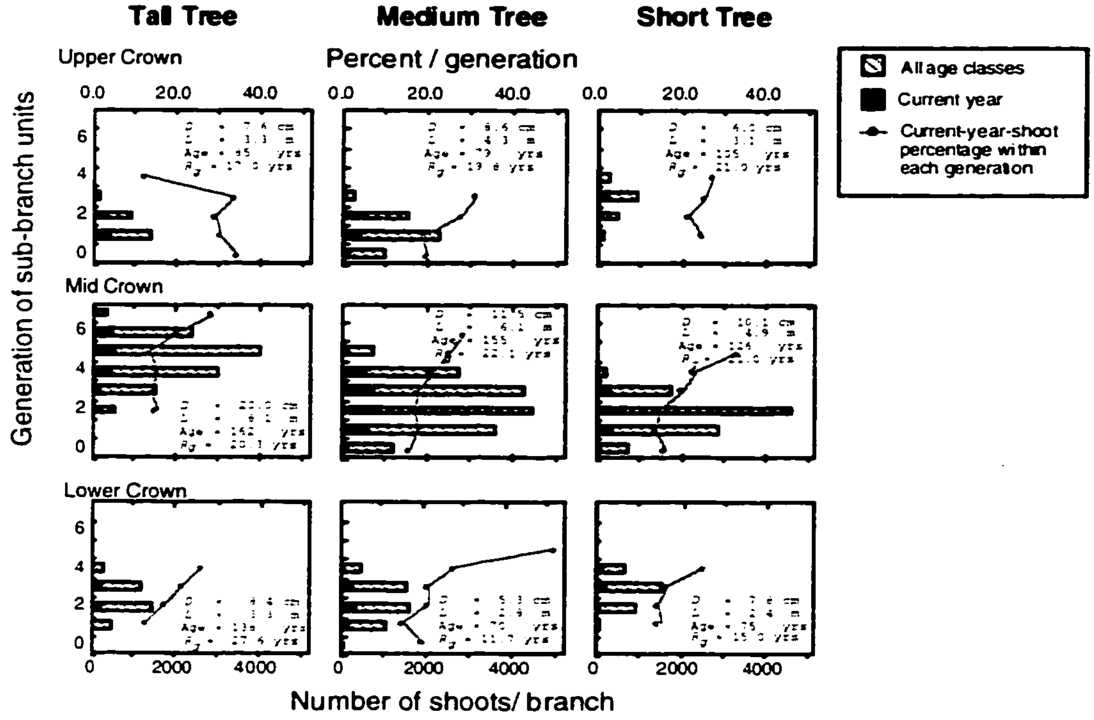

Figure A.2 Number of foliated shoots within branches from the upper-, mid- and lower-crown branches of the Tall Tree, Medium Tree and Short Tree of *P. menziesii*. Sample trees and branches are the same as in Chapter 3. Labels 0 through 6 on the vertical axis indicate generations of sub-branch units with parts of the branch originating from the terminal bud that grew out of the trunk as generation 0. Circles with lines indicate percentages of current-year shoot numbers within each generation. Diameter (*D*), length (*L*), age, and the average production rate of new generations (R_g) are also shown for each branch.

Figure A.3 Epicormic branches (A) can be distinguished form original branches (B) by a combination of distinguishing characteristics: smooth bark texture, tangent angle of attachment to the trunk, occurrence in multiple numbers within a small area of the trunk, and smaller diameter relative to nearby original branches.

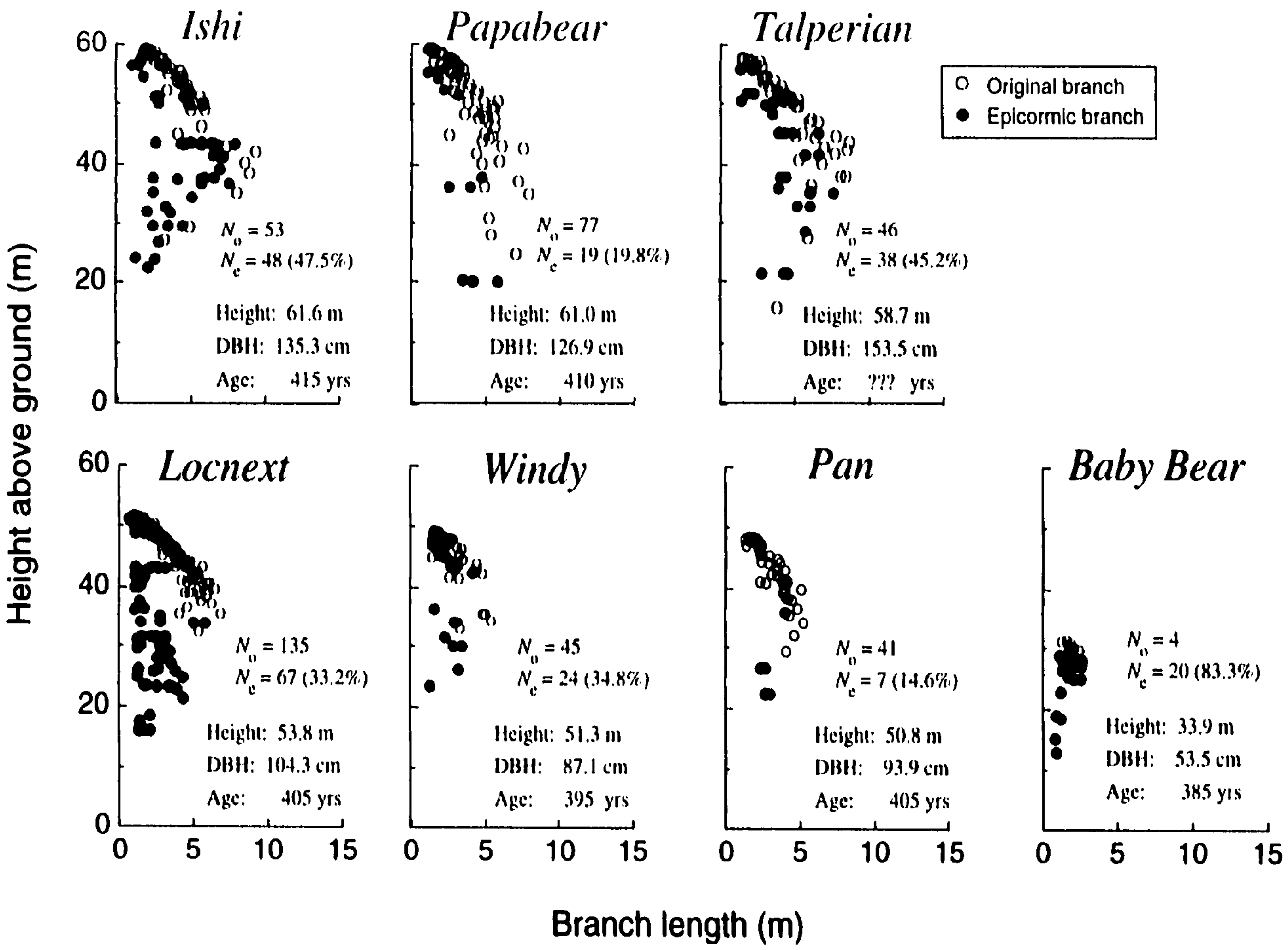

Figure A.4 Vertical distribution of branch lengths showing crown profiles of seven old-growth *P. menziesii* trees. Epicormic branches (filled symbols) form an inner crown within the outer crown created by original branches (open symbols). The number of original branches (N_o) and the number and percentage of epicormic branches (N_e) are also shown for each tree.

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