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Comparative Crown Form and Branching Pattern of Four Coexisting Tree Species in an Old-growth *Pseudotsuga-Tsuga* Forest

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Abstract

We compared crown expansion rates and branching pattern among four coexisting canopy tree species in a 450-year-old *Pseudotsuga menziesii* – *Tsuga heterophylla* forest in southwestern Washington State, USA. Branch terminal shoot elongation and new shoot production were low at all canopy levels for trees of all species taller than 45 m despite favorable light conditions in the upper canopy. This indicated that the negative effects of physiological aging and increasing size are more important in controlling crown expansion rate than local light conditions. Branch terminal shoot elongation rates were high for the upper-crown branches of short trees despite low irradiance. There may be little crown competition among tall trees in this forest, whereas for the short trees, allocation to shoot elongation in the upper-crown is important for crown expansion and survival. Branching patterns were similar among *P. menziesii*, *A. amabilis*, and *A. grandis*. These three species showed excurrent, symmetrical branching patterns with few internodal shoots and less differentiation among shoots in their elongation rate and bifurcation ratio. In contrast, *T. heterophylla* showed a reiterating branching pattern where distal shoots on each annual increment were longer and had higher bifurcation ratios than the proximal shoots. When compared with young trees, old trees of *T. heterophylla* maintain a similar branching pattern, whereas, branching pattern of old *P. menziesii* trees is markedly different from that of young trees. The changes in branching pattern from young to old *P. menziesii* trees reflect morphological acclimation to changing stand light conditions as shade-tolerant species invade the stand. This, combined with initial dominance in the upper-canopy where crown competition is less intense, may contribute to the long-term survival of *P. menziesii* in old-growth forest.

Key Words: Canopy dynamics, Crown competition, Crown expansion rate, Species coexistence

Introduction

The temperate coniferous forests of the Pacific Northwest Coast of North America have some of the largest and longest-living trees in the world (Waring and Franklin 1979). In the mid-elevation coniferous forests of this region, *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* (coastal Douglas-fir) is the pioneer species that invades soon after a large-scale disturbance. Forest succession generally proceeds 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). *P. menziesii* is a long-lived pioneer species that can live over 1000 years and coexist for centuries with the late-successional species (Franklin and DeBell 1988).

P. menziesii dominates 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*

continues to survive in the upper canopy for up to 800 years (Gholz *et al.* 1976, Stewart 1986a, Stewart 1986b, Franklin and DeBell 1988, Spies *et al.* 1990, Easter and Spies 1994). 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 taller than 50 m 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. They 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. Ishii and Ford (2002) proposed that sustained dominance in the upper canopy contributes to the long-term survival of *P. menziesii* allowing it to escape competition from the shade-tolerant late-successional species.

Stand light conditions in old-growth forests are markedly different from that of younger stands (Parker 1997). For *P. menziesii* to survive into late-successional

stages, it must acclimate to changing light conditions as succession proceeds and shade-tolerant species invade the stand. Crown form of old *P. menziesii* trees is markedly different from that of young trees (Franklin *et al.* 1981, Ishii and McDowell 2002), and this may reflect morphological acclimation to old-growth stand conditions. At a smaller morphological scale, we observed that branching pattern of old *P. menziesii* trees is also markedly different from that of young trees. Young *P. menziesii* trees show vigorous shoot elongation and very high rates of new shoot production. Owens (1969) found that shoots on branches of 10- to 50-year-old *P. menziesii* may produce as many as five to six vegetative buds each year. In old trees, terminal shoots of branches produce two to three new shoots each year, and lateral shoots seldom bifurcate (Fig. 1, see color plate). The simplified branching pattern of old *P. menziesii* trees is similar to the true firs (*Abies* species), which are very shade-tolerant, late-successional species. Because branching patterns reflect species' strategies for shoot and foliage display (Fisher 1986, Farnsworth and Niklas 1995, Yagi 2000), the differences in branching pattern between young and old *P. menziesii* trees may reflect morphological acclimation to late-successional stand light conditions.

In this study, we used the Wind River Canopy Crane to make direct, non-destructive, and repeated measurements to compare rates of crown expansion (branch extension) and branching pattern of *P. menziesii* with three coexisting late-successional species: *A. amabilis*, *A. grandis*, and *T. heterophylla*. We also compare the branching pattern of old *P. menziesii* trees with that of young trees to infer the degree of morphological acclimation of this species to late-successional stand conditions. Finally, we discuss how these crown- and branch-level architectural characteristics may contribute to the prolonged survival of *P. menziesii* 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, USA (45°49'N, 121°57'W; 300m a.s.l.). The largest trees in the stand are *P. menziesii* trees 40–60 m in height and 60–180 cm in diameter at breast height (DBH, 1.3 m). 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 nuttallii* 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. All measurements in this study were made using non-destructive methods.

A total of 312 canopy-level trees are accessible using the canopy crane. Of these, three trees from each of four species, *P. menziesii*, *A. amabilis*, *A. grandis*, and *T. heterophylla* were chosen for measurement (Table 1). Together, these four species comprise 73% of the total number of trees with DBH > 5 cm in the 4-ha study area (Freeman and Ford 2002). The three sample trees represent tall, medium and short trees of each species and were chosen based on the height distribution of the canopy-level trees. The *P. menziesii* population consisted of taller trees than *A. amabilis*, *A. grandis*, and *T. heterophylla*, so the shortest sample tree of *P. menziesii* was taller than or similar in height to the tall and medium sample trees of the latter three species.

Table 1. DBH, tree height and crown depth of tall, medium and short trees of each species sampled for measurement of branch terminal shoot elongation, shoot production, and branching pattern using the canopy crane.

Species	DBH (cm)	Height (m)	Crown depth (m)
<i>P. menziesii</i>			
Tall	166	64.8	48.2
Medium	148	57.5	40.5
Short	72	46.2	22.8
<i>A. amabilis</i>			
Tall	51	46.4	24.6
Medium	20	26.5	10.6
Short	19	19.8	9.3
<i>A. grandis</i>			
Tall	80	53.8	44.1
Medium	55	48.6	36.0
Short	27	30.5	9.6
<i>T. heterophylla</i>			
Tall	93	53.3	44.5
Medium	51	42.1	27.1
Short	27	24.7	15.9

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-, middle-, and lower-crown. A sample branch which extended farthest away from the trunk was chosen near the mid-height of each crown-level.

The light environment at each sample branch was measured using the Sunfleck PAR (photosynthetically active radiation) Ceptometer (Decagon Devices Inc., Pullman, WA, USA), which uses several PAR sensors arranged in a line to calculate average photon flux density of PAR 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 at each sample branch.

Branch extension and shoot demography

Three branch terminal shoots farthest away from the trunk were selected for measurement of terminal shoot elongation rates (Fig. 2A). Distances between annual increments at each terminal shoot were measured and averaged over the three-year study period for each branch. Two of the three branch terminals were chosen at each branch for analysis of branching pattern. A branch map (Powell 1977, Stoll and Schmid 1998) was created by following each terminal shoot basipetally noting all annual budscale scars on the primary axis and higher-order axes as far back as live foliage was present on the primary axis (Fig. 2B). 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 (hereafter "shoots" are equivalent to annual axis increments) were conducted twice per year: in early May before bud break (spring census); in late October following the growing season and autumn needle fall (autumn census). At each census, terminal shoot elongation was measured and all shoots on 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 total number of foliated shoots of the two branch maps at each crown-level:

(1) New shoot production rate (r_T):

$$r_T = n_{0,T} / n_{0,T-1} \quad (1)$$

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

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

$$R_T = N_T / N_{T-1} \quad (2)$$

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

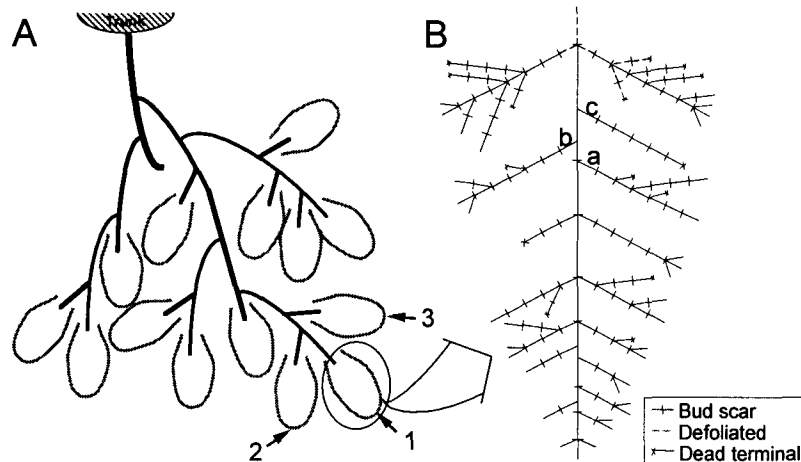


Fig. 2. Schematic diagrams illustrating the sampling units. Three branch terminal shoots farthest away from the trunk (A, arrows 1-3) were selected for measurement of terminal shoot elongation rates. Of these, two were chosen for measurements of shoot demography and branching pattern using branch maps (B). The primary axis was defined by following the branch terminal shoot basipetally as far back as foliage was present. The position of each secondary axis was identified basipetally by the primary axis annual increment and relative position of the secondary axis within the annual increment. For example axes 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 secondary axes were measured to quantify branching pattern.

Branching pattern

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

$$Rb_T = n_k / n_{k+1} \quad (3)$$

where n_k is the number of shoots of age k . Bifurcation ratios for each year of growth were averaged to obtain mean bifurcation ratio for each secondary axis (Rb).

Results

Branch extension and shoot demography

Relative PAR decreased from upper- to lower-crown in all trees (Fig. 3a). For all trees of *P. menziesii* and the tall and medium trees of *A. amabilis*, *A. grandis*, and *T. heterophylla*, relative PAR decreased markedly from upper- to lower-crown. For the short trees of *A. amabilis*, *A. grandis*, and *T. heterophylla* changes in

relative PAR from the upper- to lower-crown were relatively small.

For all trees of *P. menziesii*, the tall 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⁻¹) at all crown-levels despite large decreases in relative PAR from upper- to lower-crown (Fig. 3b). In contrast, for the short trees of *A. amabilis*, *A. grandis*, and *T. heterophylla*, branch terminal shoot elongation rates were high (8.37 - 12.53 cm yr⁻¹) 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 tall and short trees.

New shoot production rate (r) and net increase rate of all foliated shoots (R) during the study period generally decreased from upper- to lower-crown in most trees with the exception of the tall tree of *T. heterophylla* where the opposite trend was observed (Fig. 3c and d). For all trees of *P. menziesii* and for the tall 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 marked decrease in relative PAR. Of these, the tall tree of *T. heterophylla* showed the greatest relative change in r and R (26.9% and 18.2% increase from upper- to lower-crown). For the medium trees of *A. amabilis*, *A. grandis*, and the medium and short trees of *T. heterophylla*, decreasing trends in r and R from upper- to lower-crown corresponded well with

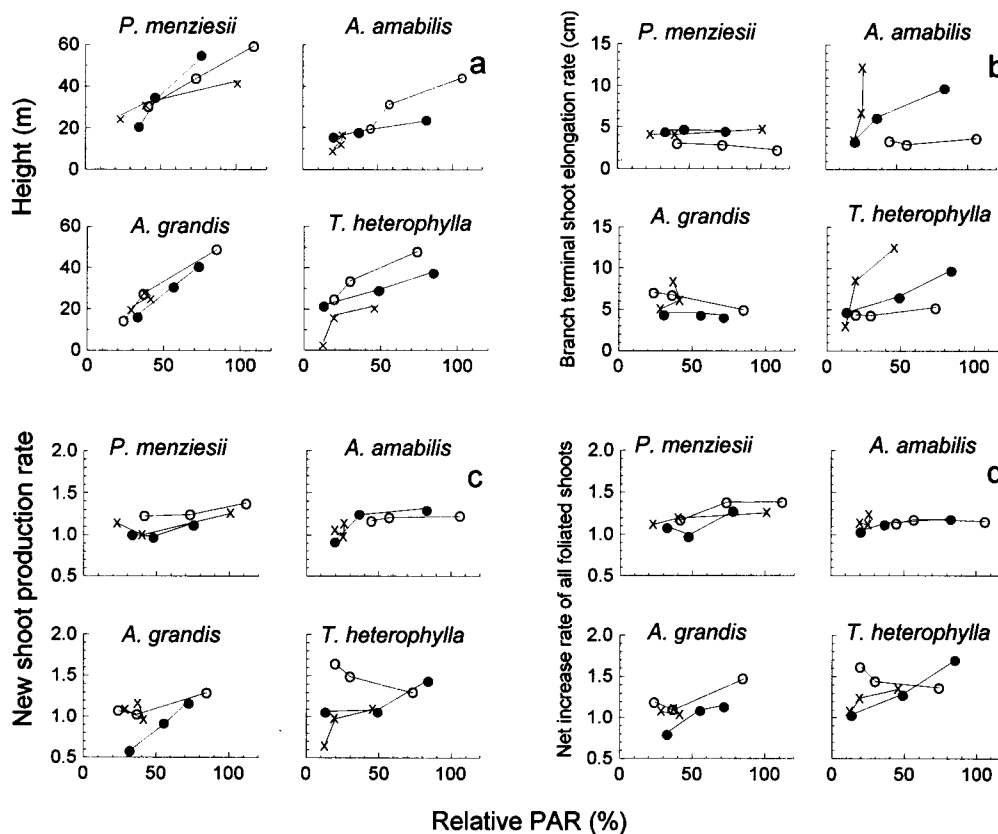


Fig. 3. Relationships between relative PAR and branch height (a), branch terminal shoot elongation rate (b), new shoot production rate (c), net increase rate of all foliated shoots (d) for tall (○), medium (●) and short (×) trees of each species.

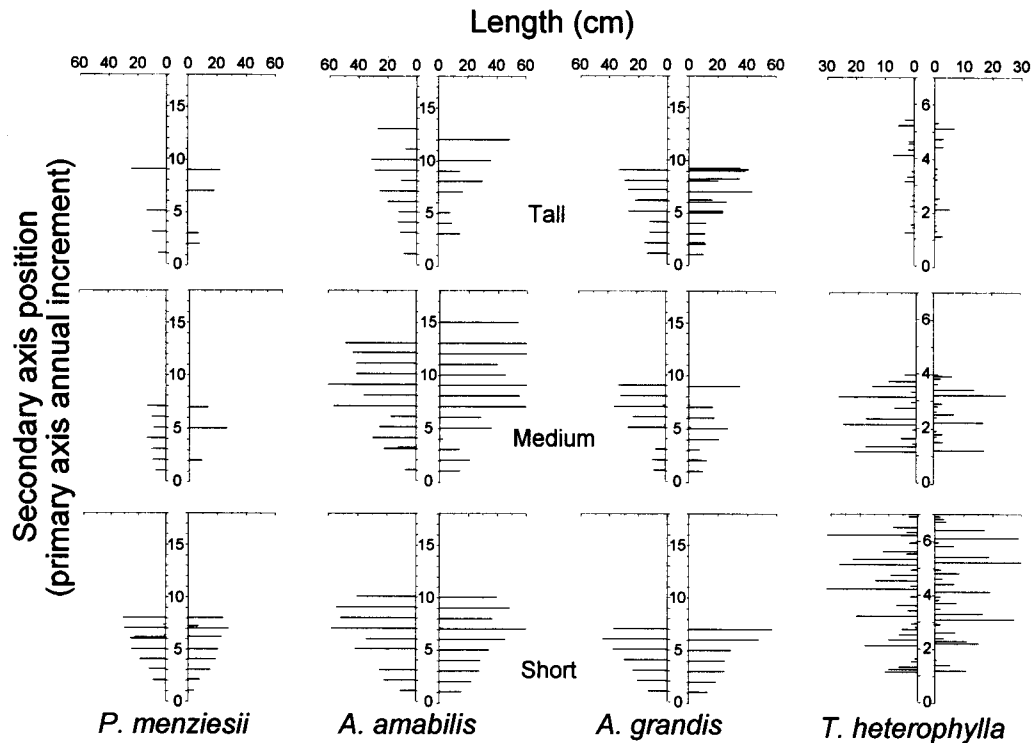


Fig. 4. Length and position of secondary axes along the left and right sides of the primary axis of the branch tip, illustrating branching patterns for the upper-crown branches of tall, medium and short trees of each species. The branch terminal is at the bottom of each graph, and secondary axis positions are marked by the primary axis annual increment. Note different horizontal axis scales for *T. heterophylla*.

decreases in relative PAR. Of these, the medium tree of *A. grandis* showed the greatest relative change in r (49.2% decrease from upper- to lower-crown), while the medium tree of *T. heterophylla* showed the greatest relative change in R (61.0% decrease from upper- to lower-crown). For the short trees of *A. amabilis* and *A. grandis*, r and R changed little from upper- to lower-crown as did PAR. The short tree of *A. amabilis* showed the greatest change in r (7.1% decrease from upper- to lower crown), while the short tree of *A. grandis* showed the greatest change in R (17.2% decrease from upper- to mid-crown).

Branching pattern

Overall branching patterns were similar among *P. menziesii*, *A. amabilis* and *A. grandis*, in contrast to *T. heterophylla* (Fig. 4). The former three species generally had two to three secondary axes per primary axis annual increment, and showed an excurrent, symmetrical branching pattern where secondary axis length increases basipetally along the primary axis. *T. heterophylla* produced many more secondary axes per primary axis annual increment than did the other three species. The internodal secondary axes of *T. heterophylla* originated from axillary buds at internodal positions on the primary axis and generally became shorter in length basipetally within each primary axis annual increment. This pattern was strongest for the short tree. As a result, *T. heterophylla* showed a reiterating pattern in secondary axis length along the

primary axis where the distal secondary axes on each primary axis annual increment are longer than the proximal secondary axes.

Relative frequency distributions of elongation rates and mean bifurcation ratios (Rb) of secondary axes were also similar among *P. menziesii*, *A. amabilis*, and *A. grandis*, in contrast to *T. heterophylla* (Fig. 5). The former three species showed unimodal distributions of secondary axis elongation rates. The range of the distribution was narrower for *P. menziesii* than for *A. amabilis* and *A. grandis*. In contrast, *T. heterophylla* showed a strong positively-skewed distribution with numerous short secondary axes throughout all tree sizes and crown-levels. These results indicated less differentiation among secondary axes in their elongation rate for *P. menziesii*, *A. amabilis*, and *A. grandis*, and a clear differentiation between long and short secondary axes for *T. heterophylla*.

For *P. menziesii*, *A. amabilis*, and *A. grandis*, percentage of secondary axes whose mean bifurcation ratio (Rb) = 1 increased, and relative frequency distribution of bifurcation ratios became increasingly positively skewed from upper- to lower-crown (Fig. 6). For *T. heterophylla*, more than 30% of secondary axes 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 greater maximum bifurcation ratios than *P. menziesii*, *A.*

amabilis, and *A. grandis*. These results indicated less differentiation among secondary axes in their bifurcation ratio for *P. menziesii*, *A. amabilis*, and *A.*

grandis, and a clear differentiation between secondary axes that produce only one new shoot each year and those that produce multiple shoots for *T. heterophylla*.

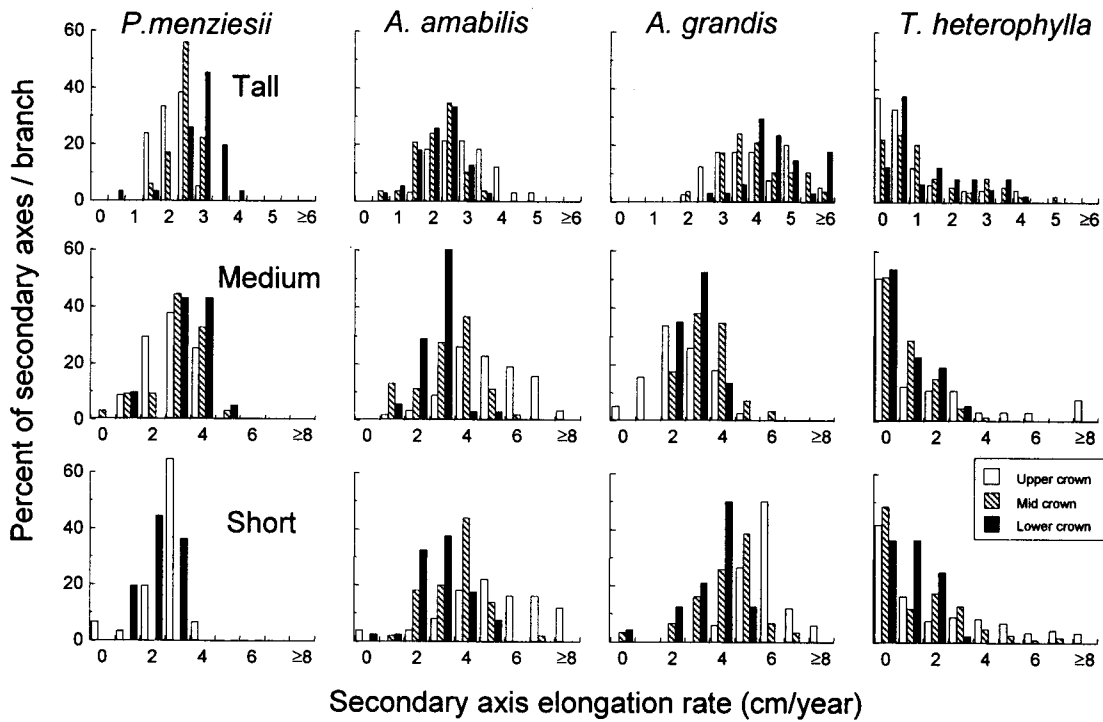


Fig. 5. Relative frequency distributions of secondary axis elongation rates of the sample trees. Note different x-axis range and intervals for elongation rates of the tall trees of each species. Elongation rates for the mid-crown branch of the short tree of *P. menziesii* could not be obtained due to damage to the branch in winter of 1999.

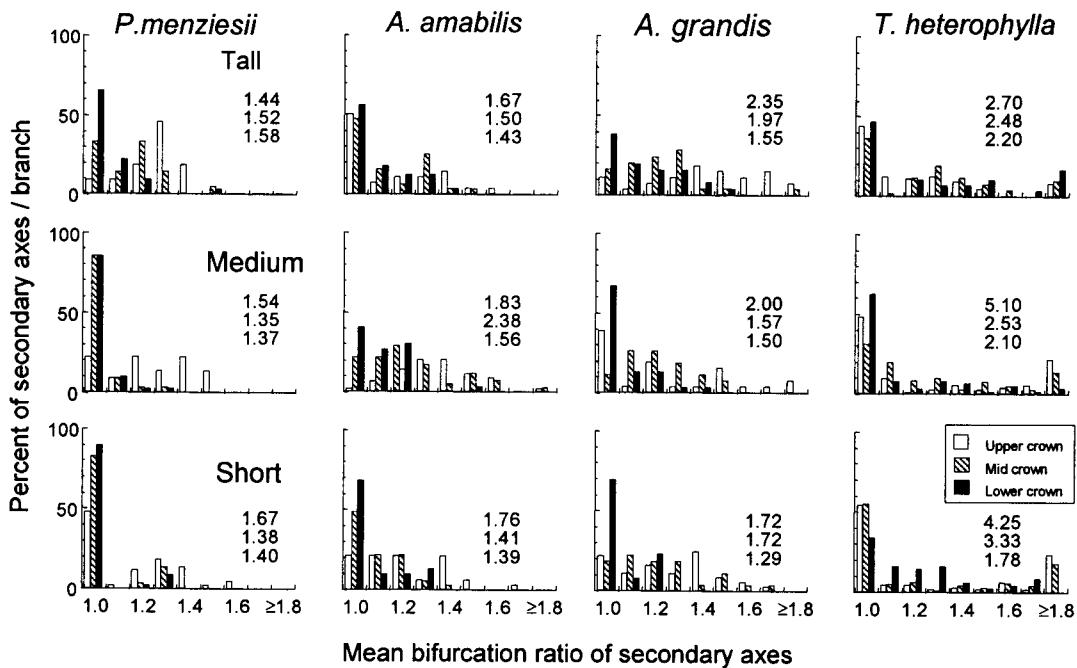


Fig. 6. Relative frequency distributions of mean bifurcation ratios (R_b) of secondary axes of the sample trees. Numbers indicate maximum mean R_b observed for upper-, mid- and lower-crown branches, respectively, of each tree. Mean R_b for the mid-crown branch of the small tree of *P. menziesii* is based on data from 1996 to 1998 (one year less than for the other branches) due to damage to the branch in winter of 1999.

Discussion

Branch extension and shoot demography

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 tall trees of *A. amabilis*, *A. grandis* and *T. heterophylla*, and the medium tree of *A. grandis*, branch terminal shoot elongation was 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 (Fig. 3). All of these trees are greater than 50 cm DBH and 45 m in height (Table 1), suggesting that effects of physiological aging, sensu Clark (1983), and increasing size and complexity may be more important in controlling crown expansion rates in tall 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 tallest trees of the shade-tolerant species in this forest. These observations suggest that rates of crown expansion are low throughout the entire crown of tall trees independent of species. Spatial distribution of trees above 40 m in this forest is sparse and many gaps exist in the upper canopy (Ishii *et al.* In press, Song *et al.* In press), implying that there may be little crown competition among tall trees in this forest.

In contrast, for short trees of *A. amabilis*, *A. grandis* and *T. heterophylla*, branch terminal shoot elongation was high in the upper-crown and decreased markedly toward the lower-crown, despite small decreases in PAR. Upper-crown branches of the short trees of the shade-tolerant species showed greater shoot elongation than lower-crown branches of the tall and medium trees despite comparatively lower PAR. Changes in shoot production rates from upper- to lower-crown for the short trees were small and corresponded to the small changes in PAR. Young trees of many conifers show excurrent crown form where shoot growth declines from upper- to lower-crown (Kozłowski and Ward 1961, Kozłowski 1971, Powell 1977, Ford *et al.* 1987). In this study, short trees had greater rates of branch terminal shoot elongation in response to small increases in light levels, indicating that crown expansion rates are high. In this forest, spatial distribution of trees in the lower canopy is dense, and tree crowns sometimes overlap with each other (Ishii *et al.* In press, Song *et al.* In press). Crown competition among short trees may be intense and crown expansion into high-light areas of the upper canopy is important for their survival. Crown expansion under low light conditions may be more efficiently achieved by allocating limited resources to branch terminal shoot elongation than to shoot production.

Branching pattern

Canham (1988) found high degrees of morphological plasticity in branching pattern and foliage display of *Acer saccharum* Marsh. (sugar maple), and proposed

that morphological acclimation may be more readily achieved than physiological acclimation because it involves less metabolic costs. In this study, the degree of differentiation between long and short secondary axes defined differences among species in their branching pattern. Despite differences in relative shade tolerance and successional status (Minore 1979), we 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 excurrent, 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 secondary axes along the primary axis, and showed less differentiation among secondary axes in elongation rate and bifurcation ratio. *T. heterophylla* has potential for indeterminate (neofomed) shoot growth (Owens and Molder 1973, Powell 1991). High degrees of differentiation were found for *T. heterophylla* among secondary axes in their elongation rates and bifurcation ratio. For *T. heterophylla*, distal secondary axes within each primary axis annual increment were long and mean bifurcation ratios were high. Maximum bifurcation ratios as high as 5.1 were found for secondary axes that produced over 100 new shoots in four years of growth. In contrast, internodal secondary axes at proximal positions within each primary axis annual increment were short and only produced one shoot in each year of growth. Similar branching patterns have been described for younger, 30 to 50-year-old *T. heterophylla* in British Columbia (Owens and Molder 1973) indicating that this species maintains a relatively constant branching pattern from young to old trees.

In contrast, morphological characteristics of old *P. menziesii* trees are markedly different from that of 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, Webber *et al.* 1985, Owens *et al.* 1985), up to 10 times that of old *P. menziesii* trees in this study. Comparative measurements made on 10-year-old, open-grown *P. menziesii* trees showed markedly different frequency distributions of secondary axis elongation rates and bifurcation ratios (Fig. 7). Young trees displayed more positively skewed distribution of secondary axis elongation rates and mean bifurcation ratio compared to old trees. Marked differences in crown form and branching pattern of old *P. menziesii* trees compared with young and mature trees indicated that this species undergoes marked morphological changes in branching

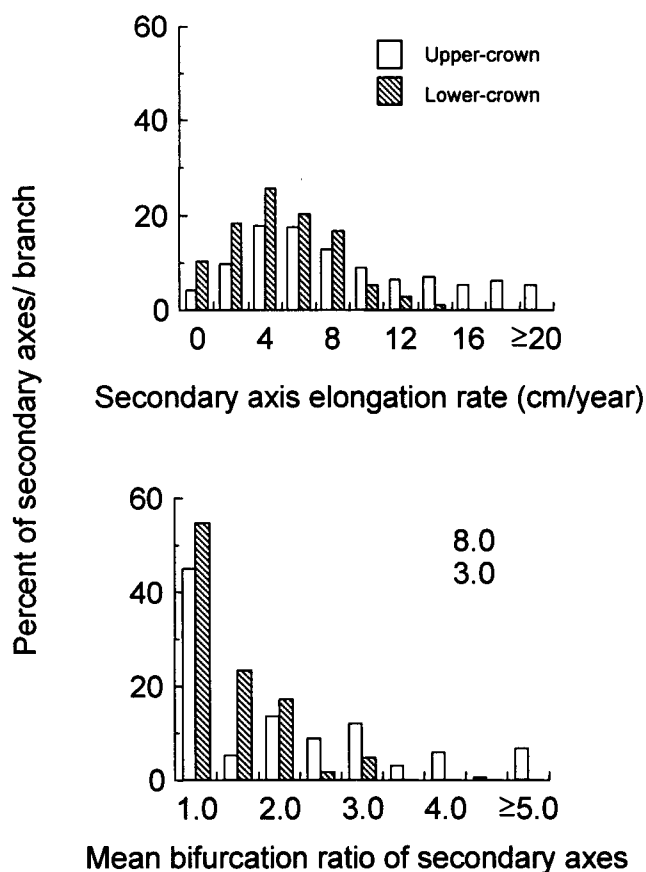


Fig. 7. Relative frequency distributions of secondary axis elongation rates and mean bifurcation ratios (Rb) for upper- and lower-crown branches of 10-year-old *P. menziesii* trees. Maximum mean Rb values were 8.0 and 3.0 for upper- and lower-crown branches, respectively.

pattern with increasing tree age.

Implications for prolonged survival of *P. menziesii*

Persistence of *P. menziesii*, a relatively shade-intolerant pioneer species, in old-growth *Pseudotsuga-Tsuga* forests may be achieved by survival in the upper canopy above the crown of more shade-tolerant, late-successional species where crown competition is less intense. The mild climate and abundant rainfall of the Pacific Northwest Coast of North America allows trees to reach canopy heights over 60 m. Height growth and crown expansion of all species in this stand becomes limited above 40–45 m in tree height. This may be an important factor contributing to the survival of relatively shade-intolerant *P. menziesii*, by allowing it to avoid competition from late-successional species in the upper-canopy. In addition, old *P. menziesii* trees show crown form and branching pattern similar to late-successional *A. amabilis* and *A. grandis*, and markedly different from young *P. menziesii* trees. This may reflect morphological acclimation with increasing tree age to changing stand light conditions as late-successional species invade the stand. Early and sustained emergence in the upper canopy where crown competition is less intense, combined with morphological acclimation with increasing tree age 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.

Conclusions

Through comparison of crown form and branching pattern among coexisting canopy tree species, we were able to make inferences about how *P. menziesii* functions as a long-lived pioneer in this forest. Branching patterns reflect species' strategies for shoot and foliage display (Fisher 1986, Farnsworth and Niklas 1995, Yagi 2000) and ultimately determine survival of individuals of different species under a given light environment. For example, in this forest, short trees and saplings of *A. amabilis* and *T. heterophylla* coexist in the lower canopy and understory with individuals of each species often growing adjacent to each other. The symmetric branching pattern and uniform shoot lengths, observed for *A. amabilis*, produces a geometric branching pattern with very little overlap among shoots of plagiotropic branches (Fig. 8A). Differentiation between long and short secondary axes in *T. heterophylla* represents an alternative strategy for efficient foliage display for branches growing under low-light conditions. Short secondary axes of *T. heterophylla* fill in space between long secondary axes, resulting in efficient packing of foliage area on plagiotropic branches (Fig. 8B). Both branching patterns result in efficient shoot and foliage display under low-light conditions. This type of

divergence in strategies for light capture may be an important mechanism for coexistence of species with different architectural characteristics. Further comparative studies of branching pattern among various species may elucidate mechanisms of species coexistence in forest ecosystems.

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Fig. 1. Branch terminal section of a 450-year-old *P. menziesii* tree illustrating the typical branching pattern.



Fig. 8. Typical branching pattern of understory trees of *A. amabilis* (A) and *T. heterophylla* (B).

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