The role of epicormic shoot production in maintaining foliage in old Pseudotsuga menziesii (Douglas-fir) trees II. Basal reiteration from older branch axes

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Abstract: Basal reiteration (epicormic shoot production from older branch axes) occurred continuously and repeatedly in branches of 450-year-old *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* (coastal Douglas-fir) trees reproducing sections of branches comprising less than 100 to as many as 10 000 foliated shoots. Basal reiteration occurred mostly from primary and secondary branch axes but also occurred from higher-order axes if lower-order axes had died back. Basal reiteration occurred in distal sections of upper-crown branches, while it occurred in more proximal sections of middle- and lower-crown branches, indicating that basal reiteration works to distribute foliage more uniformly within branches that have reached maximum size. Basal reiteration occurred repeatedly producing two to six generations of reiterated axes within branches. Less than 22.5% of foliated shoots on branches were produced by sequential branching of the primary axis. Basal reiteration also maintained a constant rate of new shoot production within the branch. Growth-ring analysis showed that basal reiteration occurred over a wide range of axis ages (5–58 years). In conjunction with previous studies, we showed that adaptive reiteration of various architectural units by epicormic shoot production is an inherent process that maintains foliage in the crown of old *P. menziesii* trees.

Key words: branch growth, branching pattern, crown maintenance, longevity.

Résumé : La réitération basale (production épicormique de tiges sur les vieux axes de branches) est survenue continuellement et répétitivement sur les branches de *Pseudotsuga menziesii* (Mirb.) Franco var. *Menziesii* (Douglas taxifolié de la côte) âgés de 450 ans, produisant des sections de branches comprenant moins de 100 jusqu'à 10 000 tiges foliées. La réitération basale se produit surtout à partir d'axes raméaux primaires et secondaires, mais survient également sur des axes d'ordre supérieur, si les axes d'ordres inférieurs ont dépéri. La réitération basale se produit dans les sections distales des branches de la couronne supérieure, alors qu'on la retrouve dans les sections plus proximales des branches de la couronne médiane et inférieure, ce qui indique que la fonction de la réitération basale est de distribuer le feuillage plus uniformément sur les branches qui ont les plus fortes dimensions. La réitération basale survient répétitivement, produisant de deux à six générations d'axes réitérés par branche. Moins de 22.5 % des tiges foliées formées sur les branches ont été produites par ramification séquentielle de l'axe primaire. La réitération basale maintient également un taux constant de production de nouvelles tiges sur la branche. L'analyse des anneaux de croissance montre que la réitération basale se produit sur une large gamme d'âges (5–58 ans). En concordance avec des études antérieures, les données montrent que la réitération adaptative de différentes unités architecturales par production de tiges épicormiques est un processus inhérent, qui maintient le feuillage dans la couronne des Douglas taxifoliés âgés.

Mots clés : croissance des branches, patron de ramification, maintient de la couronne, longévité.

[Traduit par la Rédaction]

Introduction

Reiteration is the process whereby architectural units are duplicated within the tree from suppressed buds (proleptic reiteration) or from growing axes (sylleptic reiteration) (Hallé et al. 1978; Bégin and Filion 1999). Reiteration often occurs by epicormic shoot production, where new units are produced when epicormic buds are released from suppression. Remphrey and Davidson (1992) found that reiteration by epicormic shoot production in *Fraxinus pennsylvanica* var. *subintegerrima* (Vahl) Fern. trees maintained photosynthetic capacity of the crown by increasing foliage area in older, inner regions of the crown. Bégin and Filion (1999) observed that epicormic shoots reiterate basic architectural

DOI: 10.1139/B02-080

units in branches of young *Picea mariana* (Mill.) BSP trees and proposed that epicormic shoot production represents "adaptive reiteration" that occurs in response to physiological needs as part of the normal development of the tree, in contrast with "traumatic reiteration", which occurs in response to exogenous stimuli, such as damage or defoliation.

Ishii and Ford (2001) showed that epicormic shoot production occurs continuously in branches of 450-year-old *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* (coastal Douglas-fir) trees and suggested that this process contributes to maintaining foliage in the crown of old trees that have reached maximum crown size. In old trees, the balance between productive and nonproductive organs becomes increasingly important for maintaining overall productivity of the crown (Remphrey and Davidson 1992). Epicormic shoot production reiterates productive organs from existing branching structure and is an efficient mechanism for maintaining crown productivity. Ishii and Ford (2001) observed that reiteration by epicormic shoot production occurs at three different spatial scales in old *P. menziesii* trees. Epicormic shoot production from older sections of the main stem reiterates new branches (epicormic branching). Epicormic shoot production also occurs on older branch axes reiterating large sections of the branch (basal reiteration). Epicormic shoot production from foliated axes reiterates architectural units comprising 20–300 foliated shoots (reiteration of shoot cluster units). These processes work together to maintain the established crown of old *P. menziesii* trees after the tree has reached maximum crown size.

This paper is a detailed description of the spatial and temporal pattern of basal reiteration from older branch axes by epicormic shoot production and complements earlier papers describing reiteration at larger and smaller spatial scales: epicormic branching from the main stem (Ishii and Wilson 2001) and reiteration of shoot cluster units (Ishii and Ford 2001). Together, these studies advance our understanding of the processes of reiteration of various architectural units by epicormic shoot production in old *P. menziesii* trees and how this process may contribute to maintaining productivity of the crown.

Study site and methods

Three *P. menziesii* trees were selected for study from a 450-year-old *P. menziesii* – *Tsuga heterophylla* (Raf.) Sarg. 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 355 m). The stand basal area is dominated by *P. menziesii* and *Tsuga heterophylla*. Other prevalent species in the stand include *Thuja plicata* Donn ex D. Don, *Abies amabilis* Dougl. ex Forbes, and *Taxus brevifolia* Nutt. See Franklin (1972) and Franklin and DeBell (1988) for a detailed description of the research area.

The *P. menziesii* trees in the stand are a cohort that established after a stand-replacing fire in the area (Franklin and DeBell 1988) and range 31–65 m in height, 41–180 cm in diameter at breast height (dbh), and 395–415 years in age at breast height (Ishii et al. 2000). Ishii et al. (2000) measured

height-growth rates and estimated maximum attainable heights of canopy tree species in this stand and suggested that the *P. menziesii* trees have reached their maximum height and crown projection area.

Destructive sampling is restricted within the Research Natural Area. Permission was granted to destructively sample no more than three branches from each of three *P. menziesii* trees. The trees were chosen to represent tall, medium and short trees based on the tree-height distribution of *P. menziesii* in the stand (hereafter Tree 1, Tree 2, and Tree 3). Height and dbh of the three sample trees were 61.6 m and 135.3 cm, respectively, for Tree 1, 58.7 m and 153.5 cm for Tree 2, and 50.8 m and 93.9 cm for Tree 3. The three sample trees were climbed in August of 1998 using the single-rope technique (Moffett and Lowman 1995) for measurement of crown characteristics. All primary branches were numbered, and branch height above ground, branch diameter, and branch length were measured (Ishii and Wilson 2001). The live crown of each tree, from the top of the tree to the lowest foliated branch, was divided into three crown levels of equal depth: upper, middle, and lower crown. Based on the diameter and length distributions of branches within each crown level, a median-sized branch was sampled near the midheight of each crown level (Table 1). Sample branches were cut at the base, carefully lowered to the ground using ropes, and transported to a nearby building for additional measurements.

Cross sections were cut from the branch base to estimate branch age by counting the number of growth rings. The branch was laid flat, and a schematic map of the branch was made noting all junctions and lengths of axes (Fig. 1*a*). Branch axes were ordered centrifugally starting with the primary axis of the branch attached to the main stem as order 1 increasing up to the foliated axes. Branch axes formed by epicormic shoot production (reiterated axes) can be distinguished by their vertical angle of insertion and much smaller diameter relative to the parent axis (Figs. 2 and 3). This is in contrast with axes formed by sequential branching (sequential axes), which form a more planar junction with the parent axis. Based on these morphological differences, each axis was distinguished into "reiterated axes" formed by epicormic shoot production and "sequential axes" formed by sequential branching. To investigate the spatial distribution of basal reiteration by epicormic shoot production, radial distance from the main stem to the base of each reiterated axis (D) was measured. This distance was divided by the branch length (BL) to obtain relative distance from the main stem:

[1] Relative distance from main stem = $D/$BL

Foliated sections of the branch were divided into "shoot cluster units" (SCU) as defined by Ishii and Ford (2001). The SCU is an architectural unit of shoot organization within branches of old *P. menziesii* trees characterized by a foliated main axis and several lateral axes (Fig. 1*b*; Fig. 3, R3). An SCU may comprise 20–300 foliated shoots. After mapping the branch and noting the position of each SCU, the foliated section of each SCU was dissected into annual increments at the budscale scars (hereafter foliated shoots) and separated into age-classes. The position of each SCU and the total number of foliated shoots in each SCU were

Table 1. Structural attributes of branches sampled from three 450-year-old *Pseudotsuga menziesii* trees.

Branch height and sample tree	Height (m)	Diameter (cm)	Length (m)	Aspect	Age estimate (years)	No. of SCUs*	No. of foliated shoots	Maximum branching order	No. of reiterated axes
Upper crown									
Tree 1	56.8	7.6	3.3	S	85	37	2 639	5	28
Tree 2	50.8	8.6	4.3	N	79	43	5 262	4	32
Tree 3	45.9	6.0	3.1	SW	105	19	2 092	5[†]	19
Mean		7.4	3.6		89.7	33	3 331		26.3
Middle crown									
Tree 1	35.4	20.0	8.1	NE	162	116	12 170	7[‡]	114
Tree 2	35.2	11.5	6.1	SW	155	157	17 324	6[†]	135
Tree 3	36.9	10.1	4.9	NW	126	87	10 451	6	77
Mean		13.9	6.4		147.7	120	13 315		108.7
Lower crown									
Tree 1	27.1	8.4	3.3	NW	138	28	3 690	5[†]	20
Tree 2	21.2	5.3	2.8	SE	70	54	4 930	5	48
Tree 3	26.8	7.8	2.4	E	75	28	3 442	5[‡]	27
Mean		7.2	2.8		94.3	37	4 021		31.7

*Shoot cluster units (SCUs) are architectural units of shoot organization within branches comprising 20–300 foliated shoots.

[†]Branch primary axis (order 1) was broken or died back.

[‡]Branch primary and secondary axes (orders 1 and 2) were broken or died back.

Fig. 1. (*a*) Schematic branch map of the lower-crown branch of a 450-year-old *Pseudotsuga menziesii* tree (Tree 3) sampled for analysis. Branch axes were ordered centrifugally starting with the primary axis of the branch attached to the main stem as order 1 increasing up to the foliated axes. Reiterated axes are indicated by arrows. Branch length (BL) is the distance from the main stem to the most distal point on the branch; *D* is the radial distance from the main stem to the base of each reiterated axis. Numbered units represent shoot cluster units (SCUs), architectural units of shoot organization consisting of a foliated main axis and several lateral axes.
(*b*) Magnified schematic diagram of one SCU. Lines perpendicular to axes indicate nodes between annual increments (bud scale scans). Thin axes and lighter foliage indicate current-year shoots. Arrows indicate epicormic shoots produced from foliated shoots (see Ishii and Ford 2001).
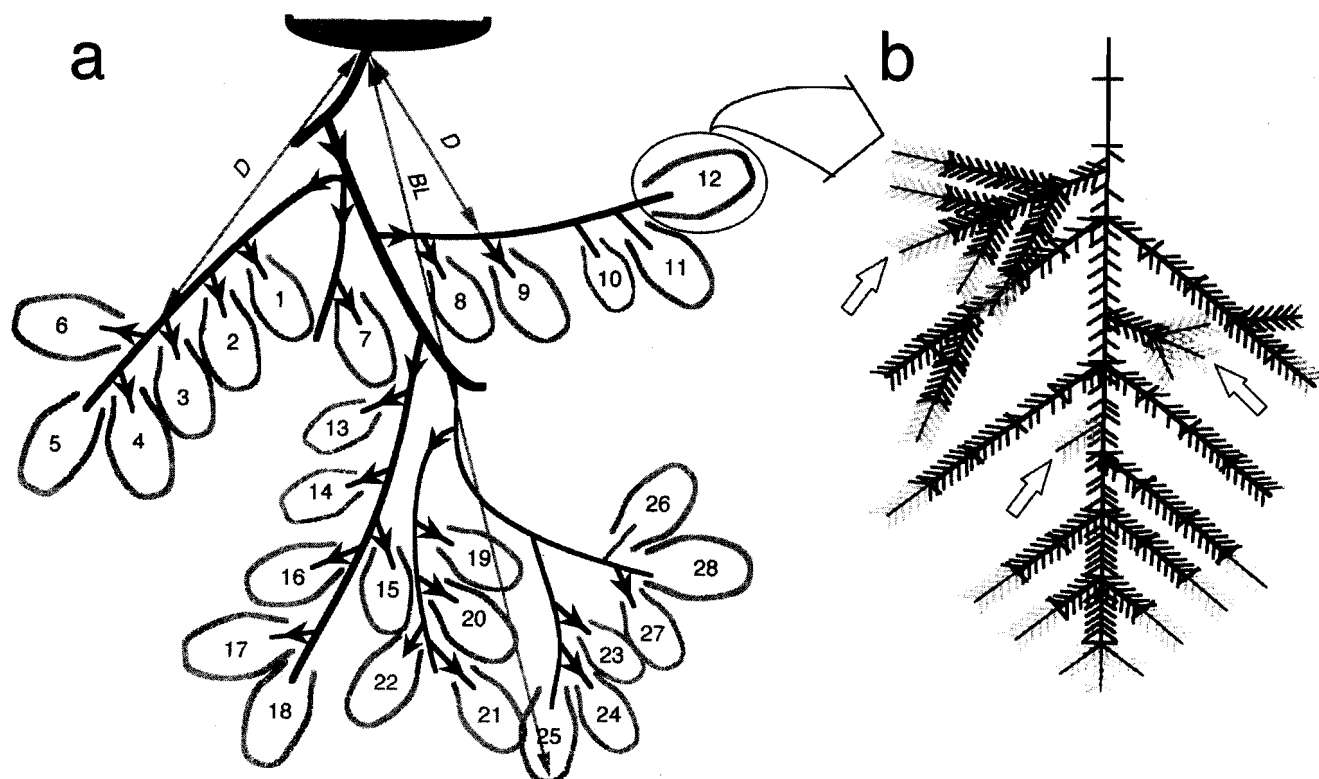
Fig. 2. Side view of basal reiterations (arrows) that occurred near the branch base in a 450-year-old *Pseudotsuga menziesii* tree. Reiter-ated axes can be distinguished morphologically by their vertical angle of insertion and much smaller diameter relative to the parent axis. In this branch, the primary axis of the branch (A1) has produced one reiterated axis (R1) near the main stem (MS). Further reit-erations have occurred on the R1 axis producing higher-order reiterated axes (R2). **Fig. 3.** View from below of multiple basal reitera-tions (arrows) formed as a result of repeated epicormic shoot production in a 450-year-old *Pseudotsuga menziesii* tree. The original primary axis of the branch (A1) grows out of the main stem (MS). The axis formed by the first reiteration (R1) is broken. The axis formed by the second reiteration (R2) on R1 has grown to comprise a large section of the branch, while the axis formed by the third reiteration (R3) on R2 is only 6–7 years old.
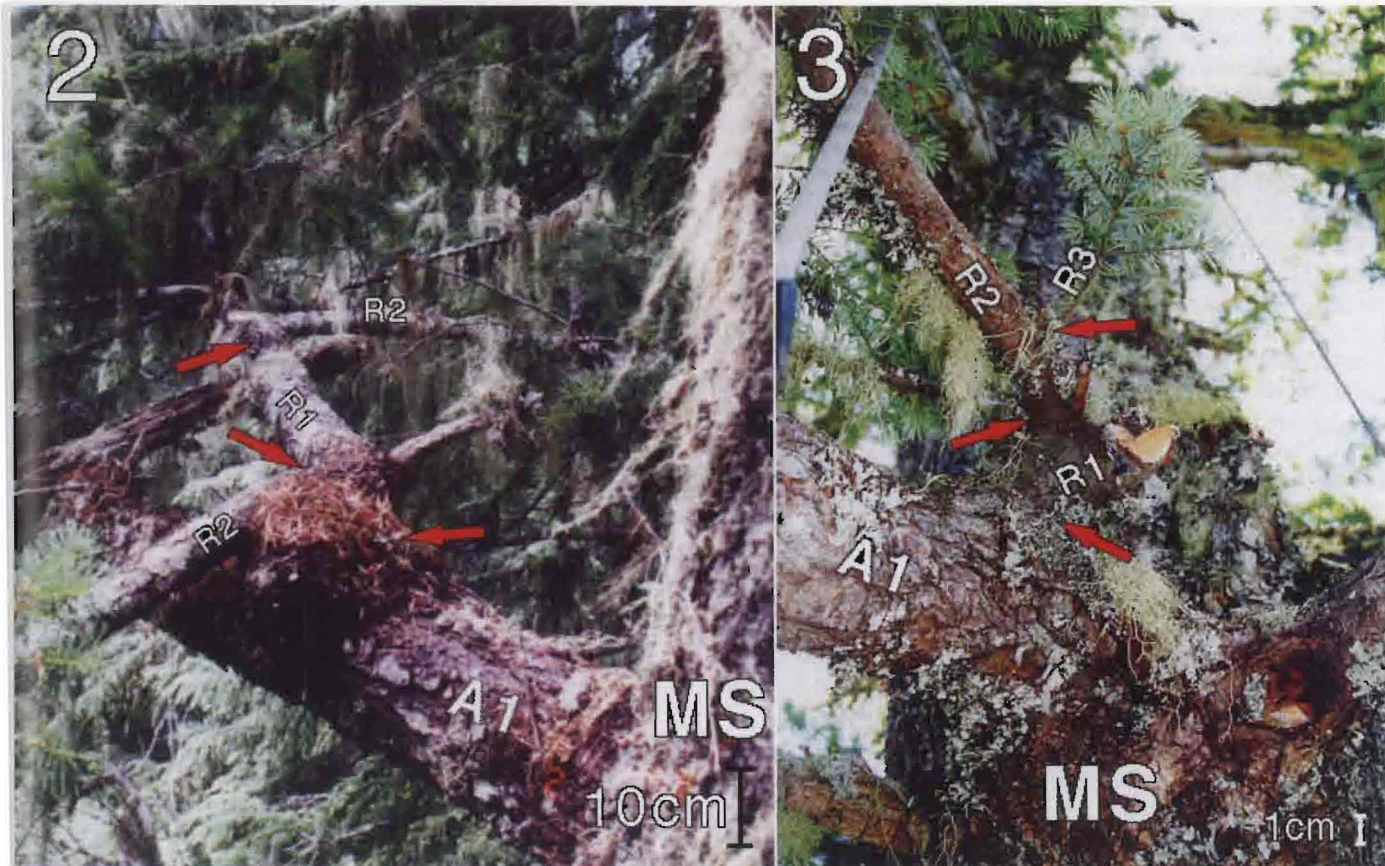
used to determine the number of SCUs and foliated shoots attached to axes of different branching orders.

Thirteen axis junctions where basal reiteration had occurred were removed from the branches for growth-ring analysis to estimate the frequency of basal reiteration by epicormic shoot production. Cross sections were cut from the distal, reiterated axis and the proximal, parent axis of each junction. The surface of the cross sections was sanded to facilitate counting of growth rings using a microscope. The difference in the number of growth rings between the parent and reiterated axis was used as an estimate of the age of the parent axis when epicormic shoot production occurred.

Statistical analyses on the data were performed using linear regression and analysis of variance (ANOVA) on Systat 5.2.1 software (Systat Inc., Evanston, Ill.).

Results

Upper-crown branches were all original branches (not epicormic branches) from the main stem, ranged in age from 79 to 105 years, and comprised 19–43 SCUs and 2092–5262 foliated shoots (Table 1). Middle-crown branches were all original branches, ranged in age from 126 to 162 years, and comprised 87–157 SCUs and 10 451 – 17 324 foliated shoots. Lower-crown branches were all epicormic branches from the main stem, ranged in age from 70 to 138 years, and comprised 28–54 SCUs and 3442–4930 foliated shoots. Maximum branching order of the sample branches were 4 and 5 for upper- and lower-crown branches and 6 and 7 for middle-crown branches. For five of the nine sample branches, the primary axis (order 1) of the branch had bro-ken or died back, and all foliated shoots originated from sec-ondary (order 2) or higher axes (Table 1, dagger symbol). For two of these five branches, secondary axes had also bro-ken or died back (Table 1, double dagger symbol). For ex-ample, for the lower-crown branch of Tree 3 (Fig. 1a), both the primary axis and secondary reiterated axis had died back, and all foliated shoots originated from five order 3 axes. Of these, four were reiterated axes and one was a se-quential axis. Dieback of lower-order branch axes contrib-uted to increasing the maximum branching order in these branches.

Reiterated axes were ubiquitous in all sample branches. The total number of reiterated axes ranged 19–32 for upper-crown branches, 77–135 for middle-crown branches, and

20–48 for lower-crown branches (Table 1). For the upper-crown branches of Tree 1 and Tree 2, the greatest number of reiterated axes occurred on order 1 and 2 parent axes, and the distribution pattern was positively skewed (Fig. 4). For the upper-crown branch of Tree 3, whose primary axis (order 1) had died back, the greatest number of reiterated axes occurred on order 3 parent axes. For the middle-crown branch of Tree 1, whose primary and secondary axes had both died back, the greatest number of reiterated axes occurred on order 4 parent axes. For the middle-crown branch of Tree 2, whose primary axis had died back, the greatest number of reiterated axes occurred on order 3 parent axes. For the middle-crown branch of Tree 3, which had an intact primary axis, the greatest number of reiterated axes occurred on order 2 parent axes. For the middle-crown branches, the distribution patterns were relatively symmetric. For the lower-crown branches, the greatest number of reiterated axes occurred on order 3 parent axes in all three sample branches. The distribution pattern was relatively uniform for the lower-crown branch of Tree 1, negatively skewed for Tree 2, and relatively symmetric for Tree 3. Dieback of lower-order branch axes shifted the mode of the distribution to higher-order axes, indicating that dieback of primary and secondary axes is associated with an increase in the number of reiterated axes observed on higher-order axes.

The spatial distribution of reiterated axes shifted from distal to proximal positions within the branch from upper- to lower-crown branches (Fig. 5). For the upper-crown branch of Tree 1, the greatest number of reiterated axes occurred between 0.5 and 0.6 of branch length, and the distribution pattern was symmetric. For the upper-crown branches of Tree 2 and Tree 3, the greatest number of reiterated axes occurred between 0.7 and 0.9 of branch length, and the distribution patterns were negatively skewed. For the middle-crown branches, the greatest number of reiterated axes occurred between 0.5 and 0.8 of branch length, and the distribution patterns were relatively symmetric. For the lower-crown branches, the greatest number of reiterated axes occurred between 0.2 and 0.5 of branch length. Distribution patterns were relatively symmetric for the lower-crown branches of Tree 1 and Tree 2, while it was bimodal for Tree 3 with modes at 0.2–0.3 and 0.6–0.7 of branch length.

For all branches, the size distribution of reiterated sections (number of SCUs and foliated shoots distal to each reiterated axis) was strongly positively skewed, indicating that small, young reiterated axes are being produced continuously (Fig. 6). For example, for the middle-crown branch of Tree 2, 106 of the 135 total reiterated axes of the branch had only one SCU distal to them. Similarly, 68 of the 135 reiterated axes had less than 100 foliated shoots distal to them, and an additional 36 reiterated axes had 101–200 foliated shoots distal to them. This indicated that the majority of the reiterated axes are young foliated axes comprising one SCU and less than 200 foliated shoots (e.g., Fig. 3, R3). The few large, old reiterated axes that had grown to comprise several SCUs and hundreds of foliated shoots occurred on lower-order axes at proximal positions near the main stem.
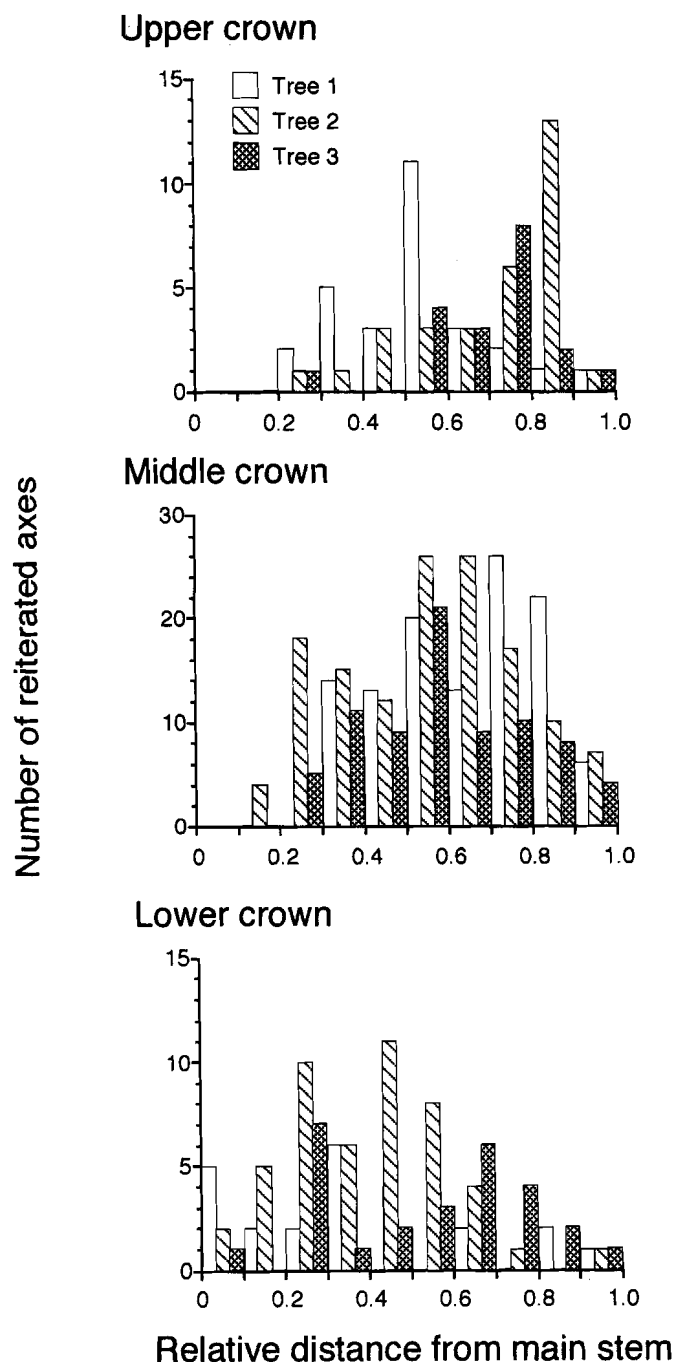
The cumulative number of reiterated axes proximal to each SCU reflects the number of repeated reiterations that occurred leading up to the foliated axis. SCUs that were produced by continuous sequential branching of the primary

Fig. 4. Number of reiterated axes occurring on parent axes of different branching order in branches of old *Pseudotsuga menziesii* trees. Asterisks above the mode indicate branches where the primary axis (order 1) has died back (single asterisk) and those where both the primary and secondary (order 2) axes have died back (double asterisk). Note the varied *y*-axis range values.
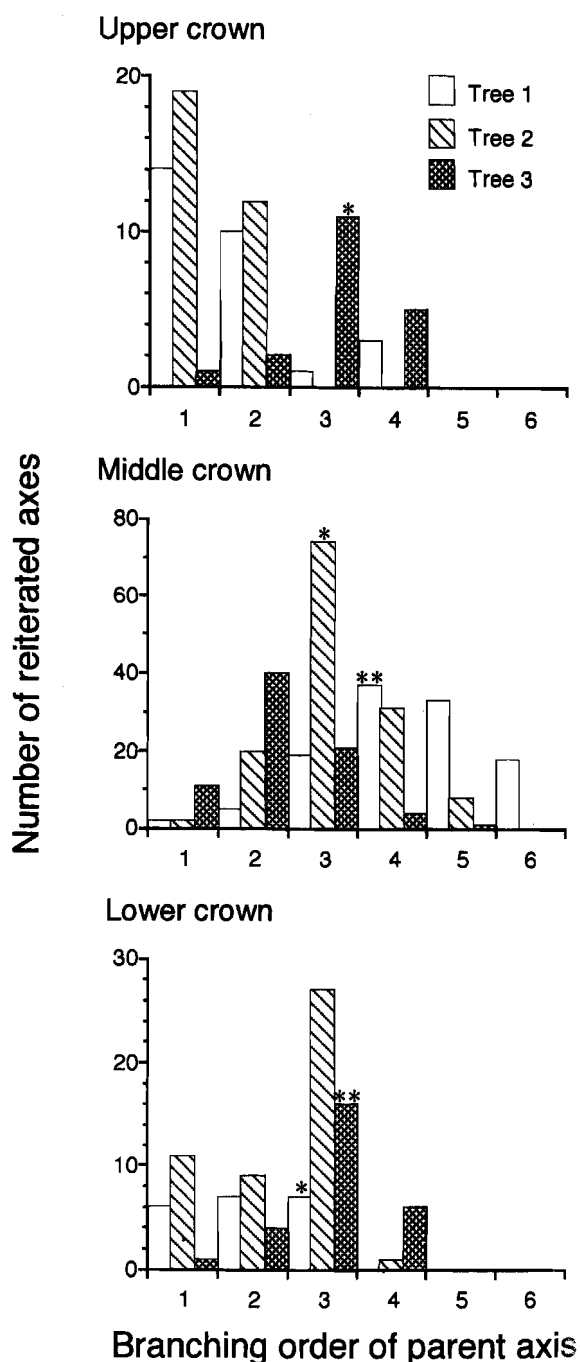
axis (order 1) of the branch should have no proximal reiterated axes, whereas SCUs produced by epicormic shoot production will have one or more proximal reiterated axes. SCUs of upper-crown branches had a maximum of two or three proximal reiterated axes, while those of middle-crown branches had a maximum of four to six, and those of lower-crown branches had a maximum of three or four proximal

Fig. 5. Spatial distribution of reiterated axes within each branch of old *Pseudotsuga menziesii* trees. Relative distance from the main stem is the radial distance from the main stem to the base of each reiterated axis relative to the total branch length (see eq. 1). Note the varied y-axis range values.

comprising 1184 foliated shoots (22.5% of the branch total) had no proximal reiterated axes. For the upper-crown branch of Tree 3, all SCUs had one or more proximal reiterated axes, indicating that all foliage on this branch had been produced by epicormic shoot production. For the middle-crown branch of Tree 1, all SCUs had two or more proximal reiterated axes. For the middle-crown branches of Tree 2 and Tree 3, most of the SCUs had one to three proximal reiterated axes, and only 12 SCUs comprising 1733 foliated shoots (10%) and five SCUs comprising 872 foliated shoots (8.3%) had no proximal reiterated axes, respectively. For the lower-crown branches of Tree 1 and Tree 3, all SCUs had one or more proximal reiterated axes. For the lower-crown branch of Tree 2, only one SCU comprising 104 foliated shoots (2.1%) had no proximal reiterated axes. These results indicate that the majority of foliated shoots on the sample branches were produced as a result of one or more basal reiterations by epicormic shoot production, and only a small percentage were produced by continuous sequential branching of the primary axis.

For all branches, there were strong linear relationships between the total number of foliated shoots and the number of current-year shoots distal to each reiterated axis (Fig. 8). This indicated that the proportion of current-year shoots in the reiterated sections of the branch is constant among large, old reiterated sections comprising several hundred foliated shoots and small, young reiterated sections comprising fewer foliated shoots. The slope of the relationship was greater for the upper-crown branches than for the middle- and lower-crown branches (ANOVA, $F = 17.66$, $P = 0.003$). For the upper-crown branches, the slope ranged from 0.246 to 0.299, indicating that 24.6–29.9% of foliated shoots in the reiterated sections were current-year shoots. The slope ranged from 0.155 to 0.186 for the middle-crown branches and from 0.175 to 0.202 for the lower-crown branches.

Age estimates of the parent axes of junctions sampled for growth-ring analysis ranged from 17 to 104 years. Age estimates for the reiterated axes ranged from 12 to 69 years (Fig. 9). The number of SCUs and foliated shoots distal to the reiterated axis generally increased with increasing age of the reiterated axis ($r^2 = 0.445$, $P = 0.01$ and $r^2 = 0.460$, $P = 0.01$, respectively), indicating that reiterated sections of the branch increase in size with increasing age. The age difference between the parent and reiterated axes is an estimate of the age of the parent axis when epicormic shoot production occurred. These values ranged from 5 to 58 years with an overall mean of 23.5 years (Fig. 10). The range of age differences was similar between order 1 and order 2 axes, indicating that both types of axes had produced basal reiterations at a wide range of ages.

reiterated axes (Fig. 7). This indicates that the number of repeated reiterations increases with increasing branch age and size. For the upper-crown branch of Tree 1, most of the SCUs and foliated shoots had one or two proximal reiterated axes, and only one SCU comprising 60 foliated shoots (2.3% of the branch total) had no proximal reiterated axes. A similar pattern was observed for the upper-crown branch of Tree 2, where the majority of SCUs and foliated shoots had one or two proximal reiterated axes, and only nine SCUs

Discussion

The results show that epicormic shoot production from older branch axes (basal reiteration) occurs continuously in branches of old *P. menziesii* trees, reiterating small and large sections of branches comprising less than 100 to as many as 10 000 foliated shoots (most of the foliated shoots on the branch). Briand et al. (1992) observed that basal reiterations occur mainly from the primary axis of branches of young *Thuja occidentalis* L. and suggested that this process

Fig. 6. Size distribution of sections of the branch reiterated by epicormic shoot production in old *Pseudotsuga menziesii* trees. The number of shoot cluster units (SCUs) and foliated shoots distal to each reiterated axis was used as a measure of the size of the reiterated section. Note the varied y-axis range values.
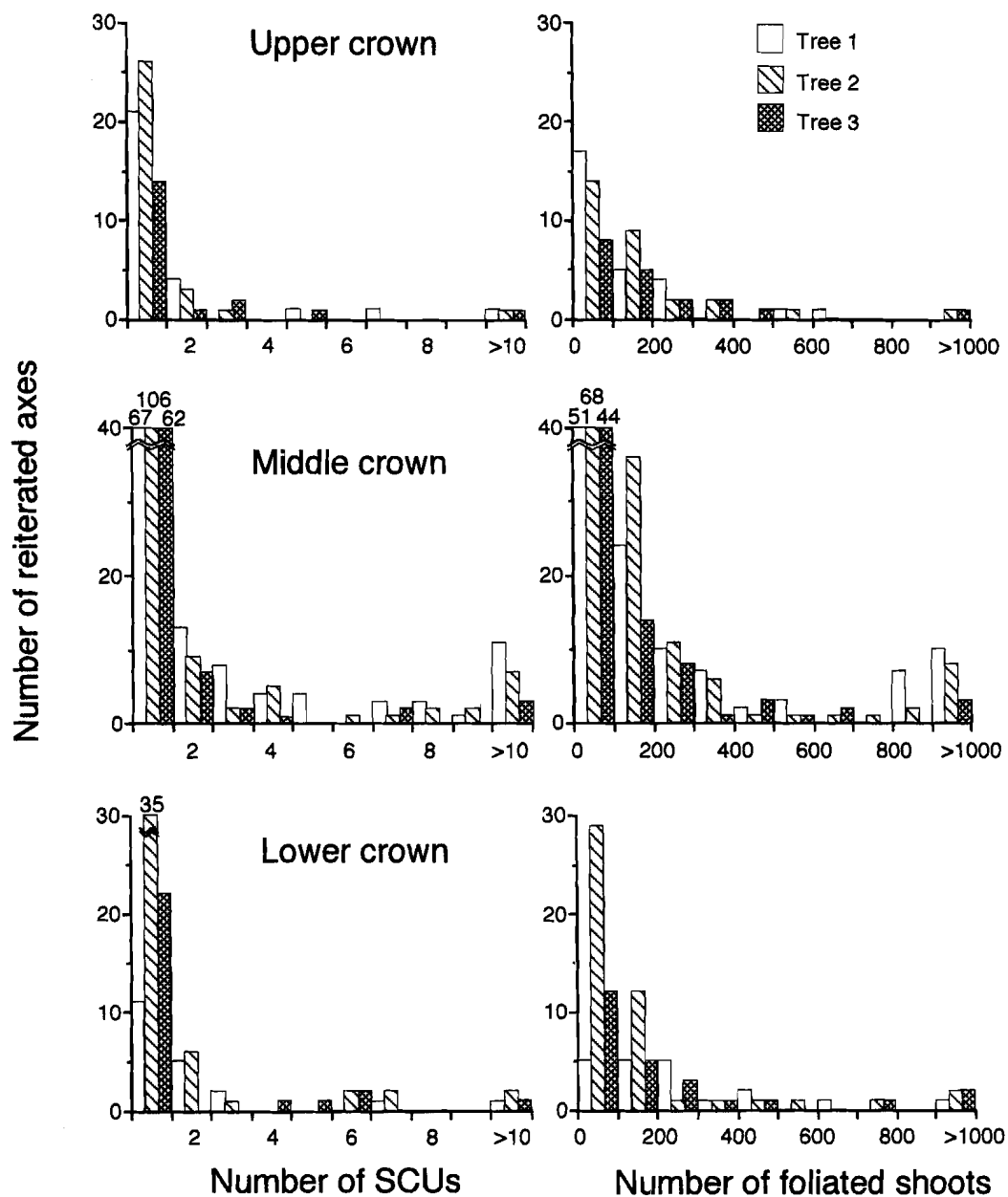

increases photosynthetic area in the inner regions of the crown where old secondary axes have abscised. Bégin and Filion (1999) observed basal reiteration to occur mainly from the primary and secondary axes of branches of young *Picea mariana*. In this study, we found that basal reiteration by epicormic shoot production occurs mainly on the primary axis of branches (order 1) and on secondary axes for young upper-crown branches where these axes are intact (Fig. 4). However, if primary and secondary axes were damaged or died back, basal reiteration occurred more often from higher-order axes. In addition, for upper-crown branches, the distribution patterns of basal reiterations across axis orders were positively skewed, i.e., concentrated on primary and secondary axes. In contrast, for middle-crown branches, the distribution patterns were symmetric, and for the lower-

crown branches, they were uniform or negatively skewed. This indicated that the frequency of basal reiterations shifts from lower-order axes to higher-order axes with increasing branch age and size and with decreasing height in the crown.

The spatial distribution of reiterated axes within the branch suggested that reiteration occurs at increasingly proximal positions within the branch with increasing branch age and size and with decreasing height in the crown (Fig. 5). Reiterated axes mostly occurred at distal positions within upper-crown branches, indicating that these branches are still expanding toward the outer crown. Upper-crown branches were relatively young and may still be increasing in size exploiting the favorable light conditions of the upper crown. Branches sampled from the middle-crown were among the largest original branches in each tree and are

Fig. 7. Number of shoot cluster units (SCUs) and foliated shoots in relation to the cumulative number of reiterated axes proximal to each SCU in branches of old *Pseudotsuga menziesii* trees. The cumulative number of reiterated axes reflects the number of repeated reiterations that occurred leading up to the foliated axis. Note the varied *x*-axis range values.
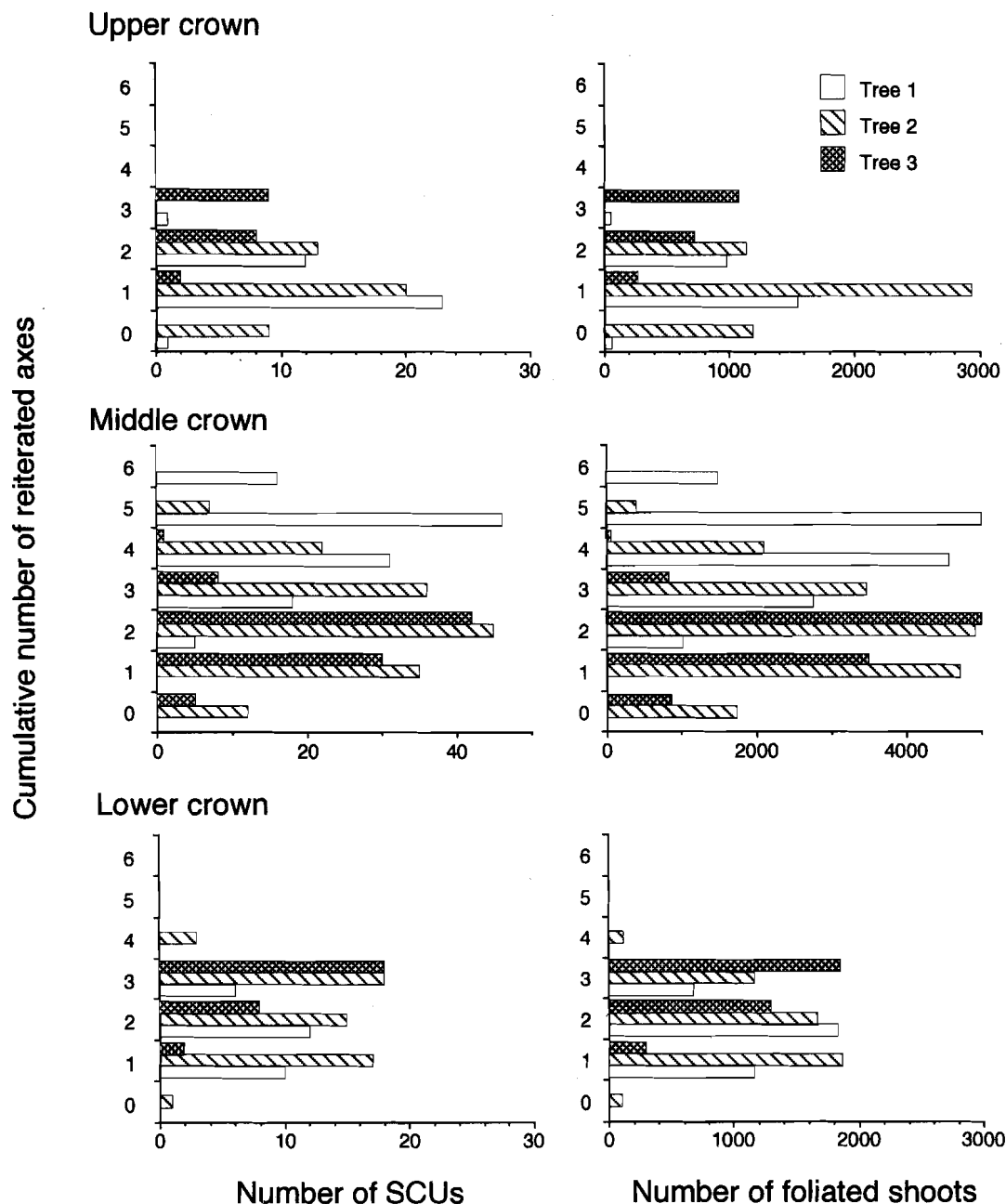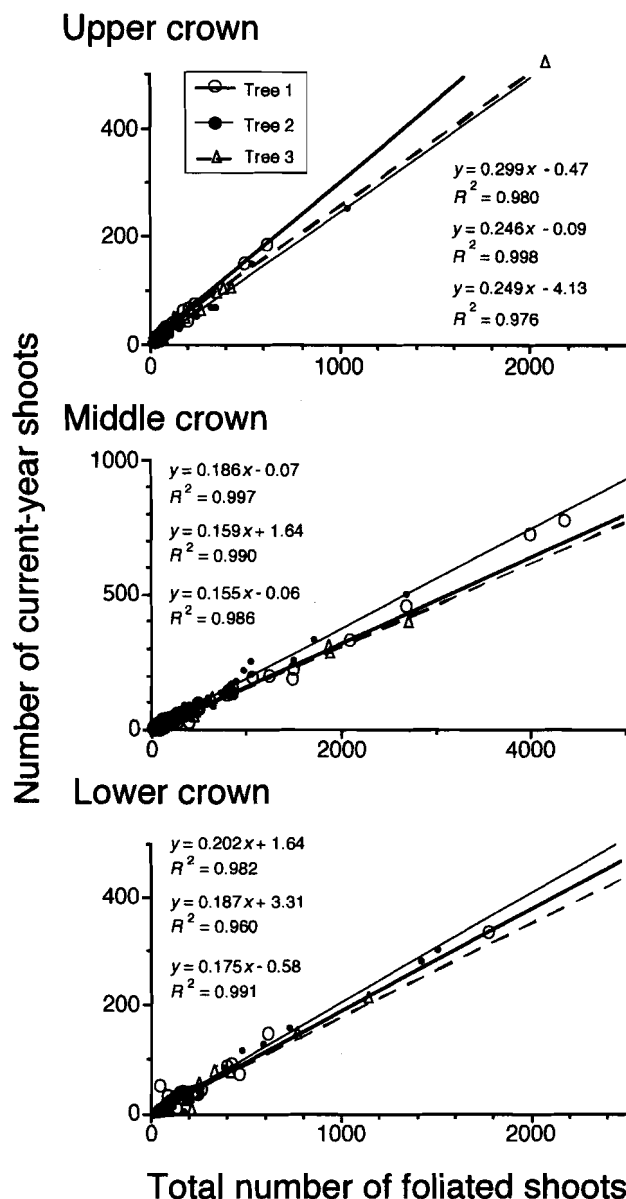

likely to have reached maximum size (Ishii and Wilson 2001). For the middle-crown branches, reiterated axes were found at more proximal positions within the branch compared with upper-crown branches. This may represent cessation of expansion growth and redistribution of foliage area to more proximal positions within the branch by basal reiteration. Lower-crown branches were epicormic branches from the main stem and were younger in age than the middle-crown branches. However, light conditions in the lower crown are uniformly dark, and this may limit branch growth. Lower-crown branches may have also reached their maximum size, and basal reiteration from proximal sections of

the branch may work to distribute foliage more uniformly within the branch.

Bégin and Filion (1999) observed that repeated reiteration produces several "generations of replicas" within branches of *Picea mariana*, suggesting that basal reiteration is a population process that continuously reproduces architectural units within branches. In this study, we showed quantitatively that basal reiteration by epicormic shoot production most often reiterates SCUs comprising up to 200 foliated shoots (Fig. 6). The strong positively skewed size distribution of the reiterated sections suggested high rates of production of reiterated axes and high mortality. Only a few

Fig. 8. Relationships between total number of foliated shoots and number of current-year shoots distal to each reiterated axis in branches of old *Pseudotsuga menziesii* trees. The slope of each relationship indicates the mean proportion of current-year shoots in the reiterated sections of each branch. The x- and y-axis range values are varied but their ratios were held constant (5:1) to facilitate comparison of slopes.

Upper crown

Tree 1
Tree 2
Tree 3

$y = 0.299x - 0.47$
$R^2 = 0.980$

$y = 0.246x - 0.09$
$R^2 = 0.998$

$y = 0.249x - 4.13$
$R^2 = 0.976$

Middle crown

$y = 0.186x - 0.07$
$R^2 = 0.997$

$y = 0.159x + 1.64$
$R^2 = 0.990$

$y = 0.155x - 0.06$
$R^2 = 0.986$

Lower crown

$y = 0.202x + 1.64$
$R^2 = 0.982$

$y = 0.187x + 3.31$
$R^2 = 0.960$

$y = 0.175x - 0.58$
$R^2 = 0.991$

Total number of foliated shoots

Number of current-year shoots

reiterated axes grow to comprise many SCUs and several hundred foliated shoots. Most reiterated axes presumably die back while still young. We also showed that basal reiteration occurs repeatedly within the branch, producing reiterated axes upon reiterated axes, adding up to as many as six repeated reiterations leading up to the foliated axis (Fig. 7). Only a small percentage of foliated shoots of old *P. menziesii* branches were produced as a result of continuous sequential branching of the primary axis, i.e., without reiteration. For some branches, all foliated shoots were attached to one or more reiterated axes, indicating that all foliage was produced by epicormic shoot production and that

Fig. 9. Age estimates of reiterated axes from the 13 axis junctions sampled from branches of old *Pseudotsuga menziesii* trees for growth-ring analysis in relation to the size of the reiterated section (number of shoot cluster units (SCUs) and foliated shoots distal to the reiterated axis).
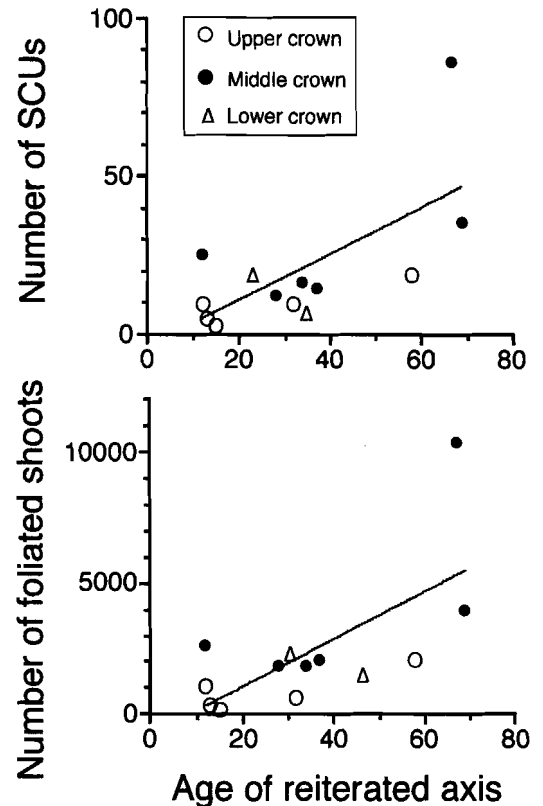

○ Upper crown
● Middle crown
△ Lower crown

Number of SCUs

Number of foliated shoots

Age of reiterated axis

Fig. 10. Age differences between pairs of parent and reiterated axes from the 13 axis junctions sampled from branches of old *Pseudotsuga menziesii* trees for growth-ring analysis in relation to the branching order of the parent axis.

○ Upper crown
● Middle crown
△ Lower crown

Parent axis branching order

Age difference
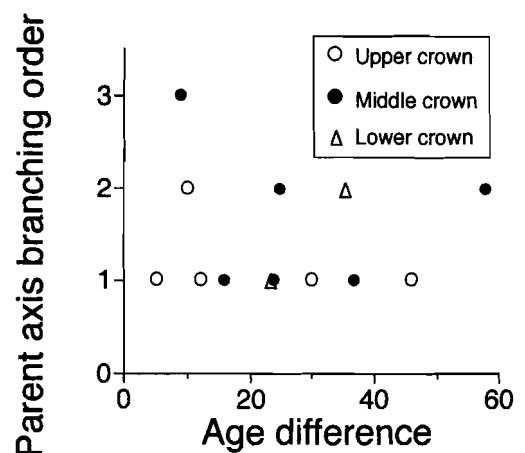
all terminal buds originating from sequential branching of the primary axis had died.

The percentage of current-year shoots within reiterated sections of the branch was constant regardless of the size of the reiterated section (Fig. 8). Both newly produced reitera-

tions comprising a few hundred foliated shoots and large reiterated sections comprising several hundred foliated shoots have the same percentage of current-year shoots. This indicated that basal reiteration maintains a constant rate of new shoot production and does not result in a decline in branch growth rate. Upper-crown branches had a higher percentage of current-year shoots than middle- and lower-crown branches, indicating that upper-crown branches are still increasing in size, while middle- and lower-crown branches may have reached maximum size. Epicormic shoots that occur in response to damage or pruning are known to have higher rates of growth and assimilation than sequential shoots (Tschaplinski and Blake 1989; Davidson and Remphrey 1994; Remphrey and Davidson 1994). Ishii and Ford (2001) showed that within SCUs, epicormic axes have higher rates of new shoot production than adjacent sequential axes. This may be because epicormic axes are replacing declining sequential axes within SCUs. At larger scales, the proportions of vigorously growing epicormic axes and declining sequential axes may balance out, resulting in constant rates of new shoot production among sections of the branch produced by basal reiteration.

Analyses of growth rings from pairs of parent and reiterated axes showed that reiterated axes increase in size with increasing age (Fig. 9) and that basal reiterations can occur on parent axes of various ages (Fig. 10). Although estimates based on the number of growth rings are approximate, as error may result from missing rings (Reukema 1959; Kershaw et al. 1990), our results suggest that reiteration can occur from epicormic shoots produced from foliated shoots (5–8 years) as well as from much older branch axes (at least 58 years old). Both primary and secondary axes produced epicormic shoots at a wide range of ages, indicating that basal reiteration occurs continuously within branches of old *P. menziesii* trees.

Ishii and Ford (2001) showed that, within SCUs, epicormic shoot production occurs most frequently from 5- and 6-year-old foliated shoots in branches of old *P. menziesii* trees. They estimated that 9–65% of annual foliage production of branches occurs on epicormic shoots. At a larger scale, Ishii and Wilson (2001) found that 15–48% of the total number of branches of old *P. menziesii* trees are epicormic branches from the main stem. They showed that epicormic branches extend crown depth and also create an "inner crown" inside the outer crown defined by the original branches. In this study, we found that basal reiteration (epicormic shoot production from older branch axes) occurs continuously and repeatedly within branches of old *P. menziesii* trees. In addition, basal reiteration may occur on axes of various branching orders and ages. Some reiterated axes may grow to comprise thousands of foliated shoots so that much of the foliage within the branch is produced as a result of one or more basal reiterations.

Previous studies have shown that epicormic shoot production in young trees occurs in response to exogenous stimuli, such as damage (Wignall et al. 1987; Wilson and Kelty 1994; Davidson and Remphrey 1994), defoliation (Carroll et al. 1993; Piene and Eveleigh 1996), and changes in light condition (Cosens 1952; Kozlowski and Pallardy 1996; O'Hara and Narayanan 2000; but see Wignall and Browning 1988). However, several studies also suggest that epicormic shoot production can occur without exogenous stimuli as part of the normal architectural development of the tree (adaptive reiteration: Bryan and Lanner 1981; Ewers 1983; Connor and Lanner 1987). Adaptive reiteration by epicormic shoot production within branches and from the main stem has been suggested as a mechanism that maintains foliage within the crown of various tree species (e.g., Bryan and Lanner 1981; Connor and Lanner 1987; Remphrey and Davidson 1992). In a recent study, Nicolini et al. (2001) found that epicormic shoot production from older, lower sections of the main stem leads to formation of an "epicormic crown" that contributes to maintaining crown productivity in suppressed *Fagus sylvatica* L. trees. Maintenance of crown productivity by epicormic shoot production may be especially important for suppressed trees that have ceased crown expansion as well as for large canopy trees that have reached maximum crown size. The ubiquity of epicormic shoot production in old *P. menziesii* trees reiterating various architectural units from clusters of foliated shoots (Ishii and Ford 2001) to large sections of branches (this study) and entire branches (Ishii and Wilson 2001) suggests that this is an inherent process that maintains crown productivity after maximum crown size and foliage biomass have been reached.

Acknowledgements

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