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(Citation)
Canadian Journal of Botany,79(3):251-264

(Issue Date)
2001-03

(Resource Type)
journal article

(Version)
Version of Record

(URL)
https://hdl.handle.net/20.500.14094/90000779

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

Hiroaki Ishii and E. David Ford

Abstract: Shoots and foliage on branches of old *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* (coastal Douglas-fir) 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 or 6 years on average. Epicormic shoot production results in 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 or 4 years of age, and peak production occurred around 6–13 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 reiteration of SCUs. Epicormic shoot production maintains shoots and foliage of old *P. menziesii* trees after height growth and crown expansion have stopped and may contribute to prolonging tree longevity.

Key words: aging, branch growth, epicormic shoots, longevity, *Pseudotsuga menziesii*, reiteration.

Résumé : Sur les branches du *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* (sapin Douglas côtier) âgé, les tiges et le feuillage sont constamment renouvelés par la production de rameaux épicormiques. Les rameaux épicormiques se forment dans toutes les parties de la couronne, et les bourgeons épicormiques restent dormants pendant 5–6 ans, en moyenne. La production des rameaux épicormique résulte de la réitération d'unités regroupées de tiges (SCUs), une unité architecturale de l'organisation des tiges au niveau des branches. Les auteurs ont identifié 5 stades de développement des SCUs, en se basant sur les structures d'âge relatives de tiges régulières et épicormiques. Les SCUs produisent des rameaux épicormiques aussi tôt qu'à 3–4 ans d'âge, et le maximum de production survient entre 6 et 13 ans. Les rameaux épicormiques se forment à l'extrémité proximale des axes principaux des SCUs, où les rameaux latéraux réguliers ne produisent plus de nouvelles tiges. Chez certaines branches de la couronne inférieure, près de 50 % des tiges et des feuilles sont constituées de tiges épicormiques. Une analyse démographiques des SCUs montre que les branches de la partie supérieure de la couronne sont encore en croissance, alors que les branches du milieu et de la base de la couronne ont atteint leur dimension maximum, et sont maintenues par réitération des SCUs. La production de tiges épicormiques maintient les tiges et le feuillage chez les *P. menziesii* âgés, après que la croissance en hauteur et l'expansion de la couronne ont arrêté, et pourrait contribuer à prolonger la longévité de l'arbre.

Mots clés : vieillissement, croissance des branches, tiges épicormiques, longévité, *Pseudotsuga menziesii*, réitération.

[Traduit par la Rédaction]

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-

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Received June 16, 2000. Published on the NRC Research Press Web site on February 27, 2001.

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Can. J. Bot. 79: 251–264 (2001) DOI: 10.1139/cjb-79-3-251

year-old *Pseudotsuga–Tsuga* forest in this region, Ishii (2000) 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* trees in the stand have reached their maximum attainable height (Ishii et al. 2000), and crown expansion has stopped (Ishii 2000). 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 stopped.

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 (*P. 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 Filion 1999).

Epicormic shoots (Fig. 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 studied more extensively in hardwoods (e.g., Kormanik and Brown 1969; Kauppi et al. 1987; Burrows 1990; Ito 1996), but also occurs in conifers (e.g., Stein 1955; Bryan and Lanner 1981; Connor and Lanner 1986; Bégin and Filion 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 suggesting 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 Filion 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.

We observed ubiquitous 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, we 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. We also discuss the implications of epicormic shoot production for persistence of individual trees of *P. menziesii* 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 – Tsuga 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 355 m). The stand basal area is dominated by *P. menziesii* and *Tsuga heterophylla*. *Thuja plicata*, *A. amabilis*, and *Taxus 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 (hereafter tall tree, medium tree, and short tree; Table 1). All *P. menziesii* trees in this stand are believed to be a cohort that 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 was 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 1 in. wide (1 in. = 2.54 cm) engineer's tape from the trunk to the farthest foliated section of the branch. The top 2–3 m 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 (hereafter upper-, mid-, and lower-crown branches; Table 1). 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.

Fig. 1. Epicormic shoots (red arrow) 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. **Fig. 2.** The shoot cluster unit is an architectural unit of shoot organization in old *Pseudotsuga menziesii* trees consisting of a distinguishable main axis (MA), formed by the extending main axis terminal bud, and several lateral branchlets. Regular lateral branchlets originate from lateral shoots produced by the main axis terminal bud, while epicormic branchlets (red arrows) originate from epicormic shoots 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 consisted of both types of shoots.

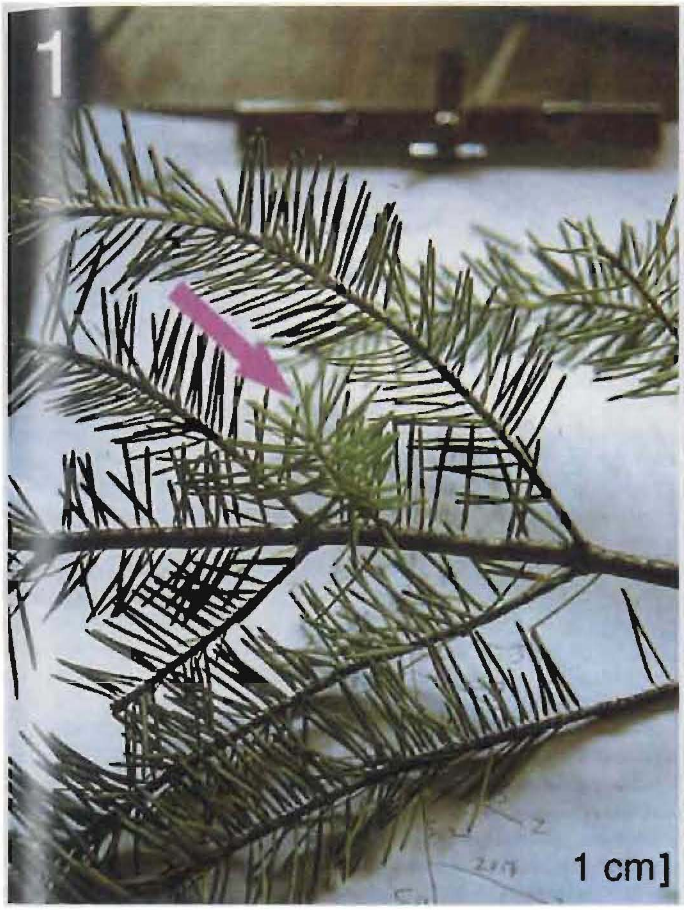
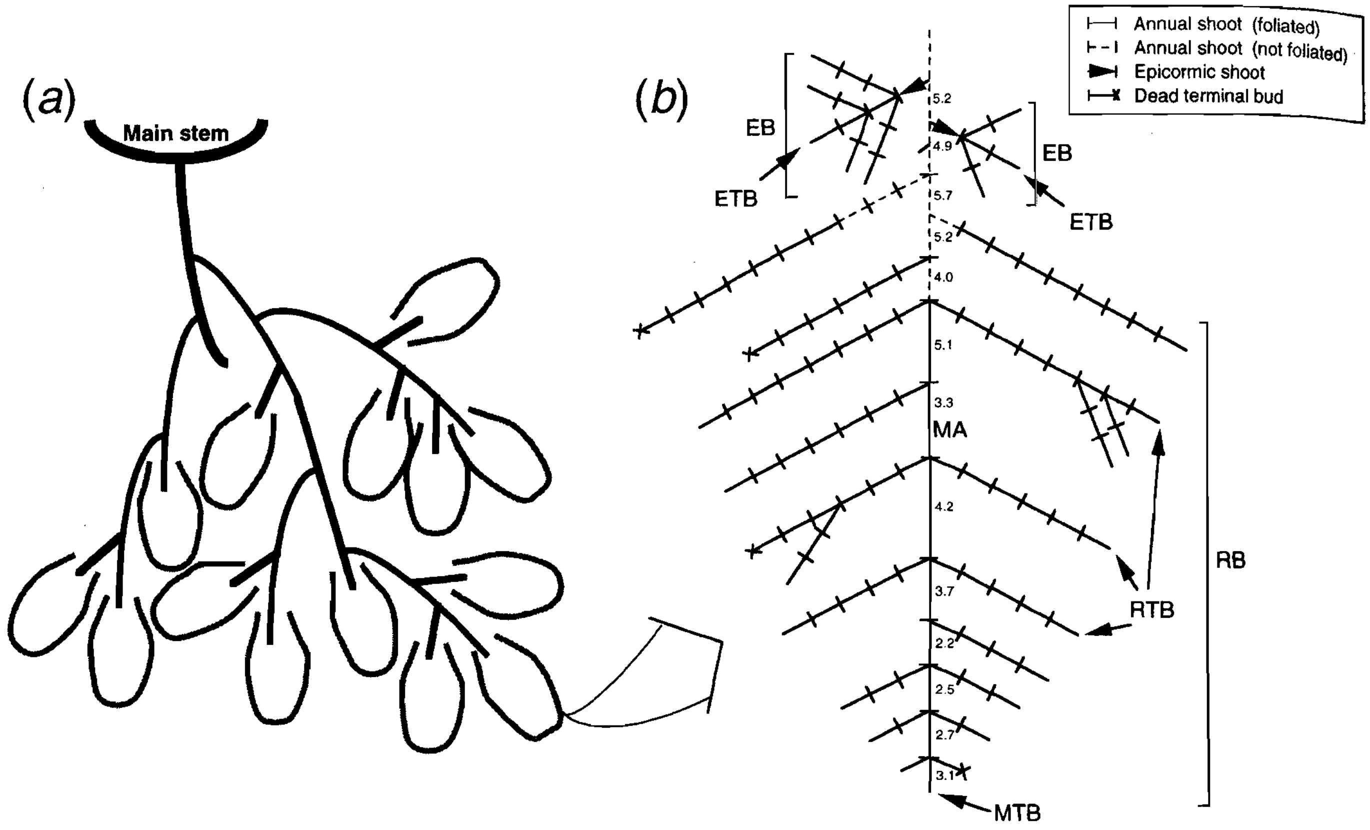


Table 1. General characteristics of sample branches of *Pseudotsuga menziesii*.

Tree branch position	Height (m)	Diameter (cm)	Length (m)	Aspect	Age estimate (years)
Tall tree (DBH, 135.3 cm; tree height, 61.6 m)					
Upper crown	56.8	7.6	3.3	S	85
Middle crown	35.4	20.0	8.1	NE	162
Lower crown	27.1	8.4	3.3	NW	138
Medium tree (DBH, 153.5 cm; tree height, 58.7 m)					
Upper crown	50.8	8.6	4.3	N	79
Middle crown	35.2	11.5	6.1	SW	155
Lower crown	21.2	5.3	2.8	SE	70
Short tree (DBH, 93.9 cm; tree height, 50.8 m)					
Upper crown	45.9	6.0	3.1	SW	105
Middle crown	36.9	10.1	4.9	NW	126
Lower crown	26.8	7.8	2.4	E	75

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 within branches of old *P. menziesii* (Fig. 2). A branch may consist of 20 to more than 150 SCUs (Fig. 3*a*). The SCU grows by forming one terminal shoot

Fig. 3. (*a*) Individual branches of *Pseudotsuga menziesii* consist of several shoot cluster units (SCUs). (*b*) A map of a typical SCU shows the main axis (MA), regular lateral branchlets (RB), and epicormic branchlets (EB) with their respective terminal buds (MTB, RTB, and ETB). Values along the main axis denote the distance between branchlets (cm). Branchlets without a live terminal bud are marked with a X at the tip.



and two or three lateral shoots each year. As a result, shoots are organized in clusters consisting of a distinguishable main axis, created by the extending main axis terminal bud, and several lateral branchlets (Fig. 3*b*). 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 annual production of terminal and lateral shoots, epicormic shoots are produced at proximal positions along the main axis of the SCU and grow to form epicormic branchlets.

Epicormic branchlets can be distinguished because they (*i*) originate from internodal positions on older main-axis parent shoots, (*ii*) grow out at vertical angles above the plain formed by the main axis and regular lateral branchlets, and (*iii*) 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 lateral branchlets usually only produce one or two new shoots per year, terminal buds of epicormic branchlets often produce three or more new shoots and form the basis of new SCUs. 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 petiolelike section at the base of the main axis separating its foliated shoots spatially from the parent SCU. We observed many SCUs that had epicormic branchlets developing into new SCUs that were still not independent from the parent SCU.

All SCUs on the sample branches were numbered, and radial distance from the branch base to the base of each SCU (hereafter 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. For SCUs that had current or 1-year-old shoots, which can be distinguished by their younger foliage, on the main axis or on regular lateral branchlets, age of the SCU was determined by counting annual bud-scale scars from these shoots to the base of the SCU. For SCUs that had no current or 1-year-old shoots on the main axis or on regular lateral branchlets, only the minimum age of the SCU could be determined by counting annual bud-scale scars from the youngest shoot on the main axis or regular lateral branchlets to the base of the SCU. In addition, all foliated shoots on the SCU were aged using bud-scale 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 4-year-old epicormic branchlet growing out of a 10-year-old parent shoot indicates that the epicormic branchlet was produced when the parent shoot was 6 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, we 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 (Fig. 3*b*). For each SCU, measurements were taken of all regular lateral branchlets and epicormic branchlets: position along the main axis (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 or epicormic) were preserved for subsequent foliage area measurement (foliage-area samples), while the remaining shoots were dried for foliage mass measurement (dry-mass samples). All needles of the remaining one half of the SCUs were sorted by shoot age-class and shoot type, oven-dried at 70°C until constant weight was reached (usually 2 or 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, Calif.). 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.) 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 mass measurement.

Needles from the foliage-area samples and dry-mass samples were oven-dried at 70°C until constant weight was reached. Dry mass 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 masses of the foliage-area sample and dry-mass 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; Fig. 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:

$$[1] \quad \mathrm{SNA} = ax + b$$

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 was 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 SCUs 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 Filion 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 2). Epicormic shoot production was observed in 56.8–100% of SCU on branches. This percentage increased from upper- to lower-crown branches in the tall and medium trees. For the short tree, the mid-crown branch had a slightly lower percentage than the upper-crown branch.

Mean frequency of epicormic shoot production (mean number of epicormic branchlets per SCU) ranged from 2.57 to 8.36 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 2). Frequency of epicormic shoot production in each SCU was positively correlated with SCU size (length × width of the foliated section) and SCU diameter (at the base of the main axis) in all branches and with SCU age in seven of eight 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 (amount of time epicormic buds are dormant on the parent shoot) ranged from 5.08 to 7.02 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 2). Timing of epicormic shoot production was positively correlated with SCU size in five of eight branches, and with SCU age in six of eight 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 (Fig. 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

Fig. 4. Examples of relationships between SCU position (distance from branch base) and specific needle area (SNA) of foliage-area samples of *Pseudotsuga menziesii*. SNA for current-year, 1-year-old, and 2-year-old needles of regular shoots from the upper-crown, mid-crown, and lower-crown branches of the tall tree are shown with linear-regression estimates of the relationship. Each point represents measurements from individual SCUs within the sample branch. These relationships were used to estimate SNAs for SCUs where foliage-area samples were not taken. The measured and estimated SNAs were multiplied by foliage dry mass to obtain foliage area estimates for each shoot type and shoot age-class of SCUs.

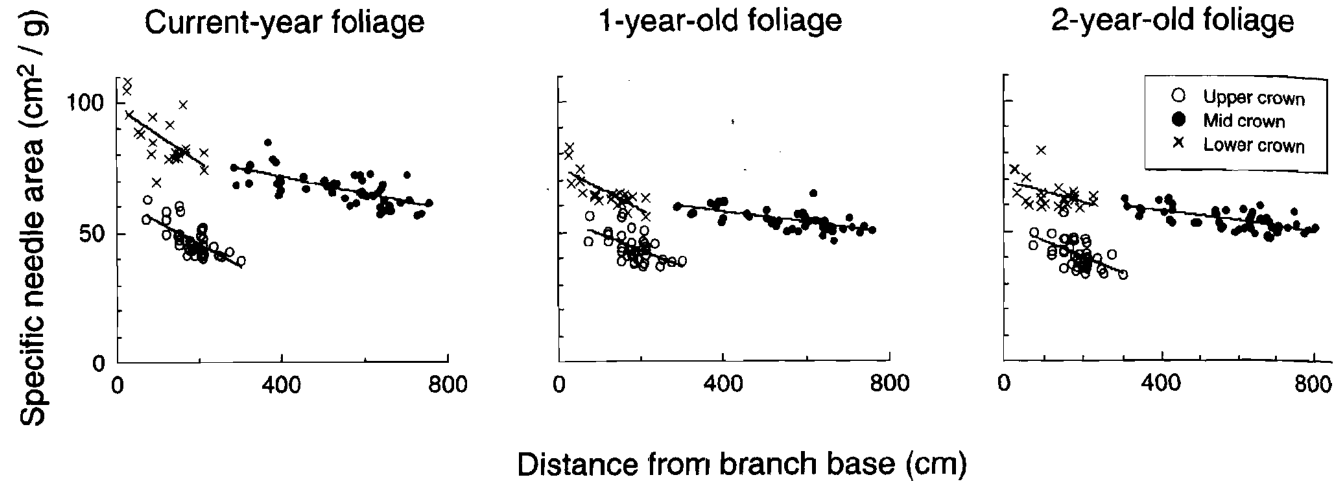


Table 2. Frequency and timing of epicormic shoot production and their correlation with size, diameter, position, and age of SCUs in *Pseudotsuga menziesii*.

Tree branch position	Total no. of SCUs	SCUs with epicormic branchlets (%)	Mean frequency (no./SCU)	r_s for frequency				Mean timing (years)	r_s for timing			
				Size[a]	Diameter	Position[b]	Age		Size[a]	Diameter	Position[b]	Age
Tall tree												
Upper crown	37	56.8	2.57x	0.499**	0.611**	–0.320	0.350*	6.72x	0.152	0.222	–0.294*	0.262
Middle crown	116	89.7	5.45y	0.561**	0.668**	0.054	0.452**	6.25x	0.214**	0.078	–0.099	0.209**
Lower crown	28	100.0	—	—	—	—	—	—	—	—	—	—
Medium tree												
Upper crown	42	81.4	4.97x	0.706**	0.611**	–0.197	0.394**	5.23x	0.205*	0.066	–0.222*	0.266**
Middle crown	157	94.3	6.03x	0.510**	0.618**	–0.177*	0.429**	5.31x	0.160**	0.147**	–0.120**	0.234**
Lower crown	54	94.4	5.90x	0.637**	0.674**	0.123	0.528**	5.08x	0.257**	0.196**	0.062	0.259**
Short tree												
Upper crown	19	73.7	5.50x	0.510*	0.835**	–0.321	0.289	5.59x	0.040	0.111	–0.111	0.106
Middle crown	86	67.8	4.55x	0.675**	0.697**	–0.227*	0.336**	7.02y	0.211**	0.192**	0.104	0.315**
Lower crown	27	82.1	8.36y	0.678**	0.611**	–0.093	0.734**	6.23x	–0.145	–0.151	–0.120	0.222**

Note: Within the same tree, branch means with the same letter (*x*, *y*) are not significantly different (ANOVA and Tukey's HSD, $P > 0.05$). r_s, Spearman's rank correlation coefficients. *, $P < 0.05$; **, $P < 0.01$.

[a] Length × width.

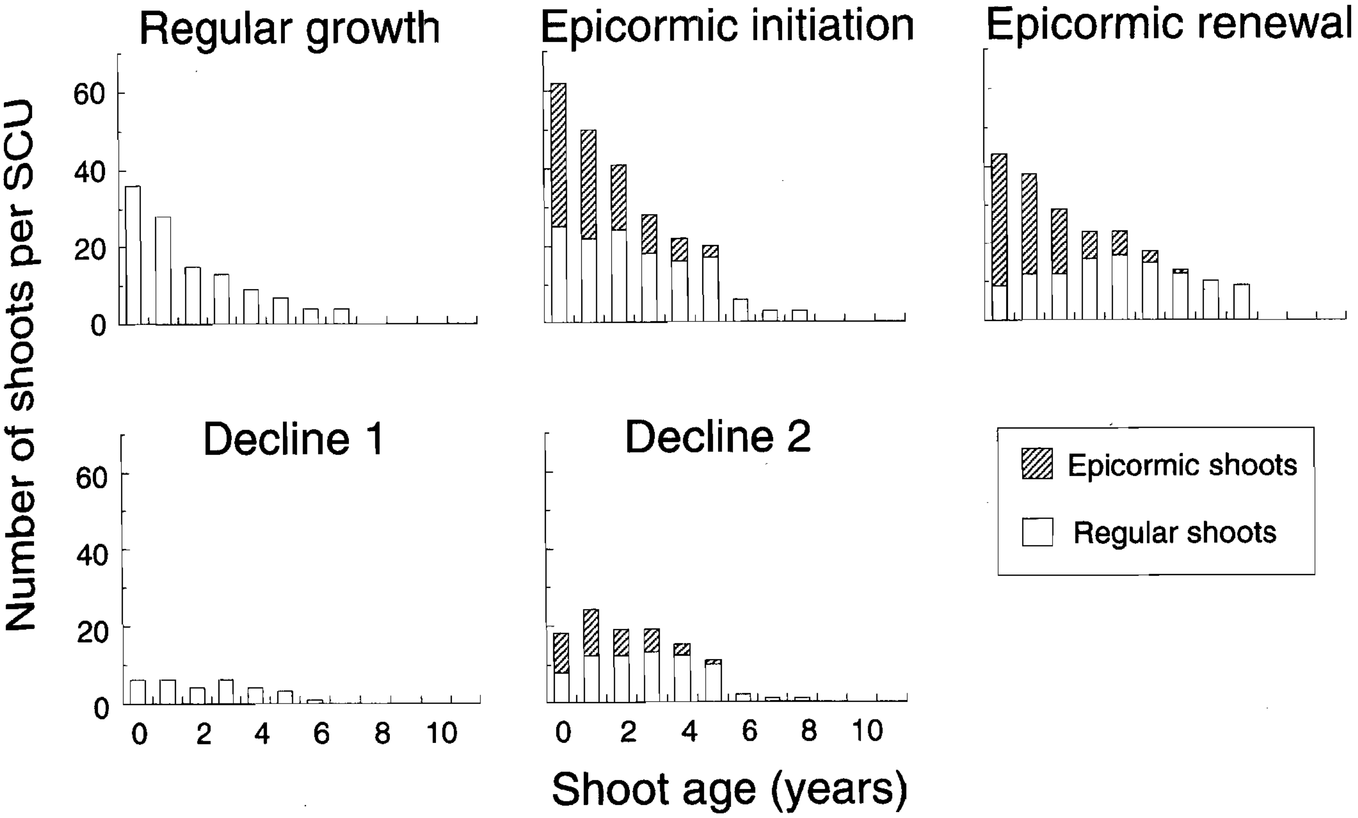
[b] Distance from branch base.

criteria, SCUs were distinguished into three phases of growth and reiteration and two phases of decline.

The three phases of growth and reiteration are as follows.

1. Regular growth phase: The SCU consists only of regular shoots showing an expanding age structure. This is the first phase of SCU development.
2. 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 SCUs first start to develop epicormic branchlets.
3. Epicormic renewal phase: The SCU consists of both regular and epicormic shoots, and regular shoots show a

Fig. 5. Examples of shoot age structures of *Pseudotsuga menziesii* 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.



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 as follows.

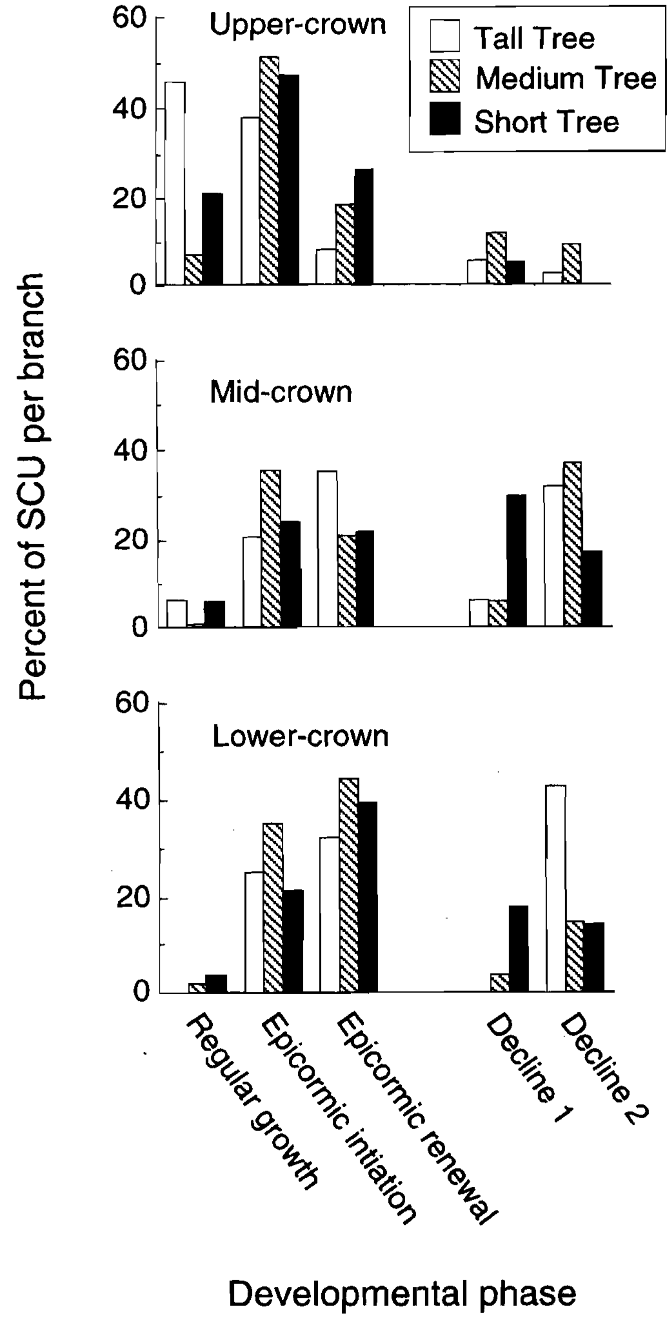
(1) Decline 1 phase: The SCU consists only of regular shoots showing a declining age structure. This phase is observed when the SCU declines without producing epicormic branchlets or after newly formed SCUs originating from epicormic branchlets become independent and the declining parent SCU has no other epicormic branchlets.

(2) 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 (Fig. 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 (Fig. 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. Ages of SCUs for the two phases of decline varied widely, and mean age was not different from the three phases of growth and reiteration. These results suggested that SCUs increase in size and age from regular growth phase to epicormic initiation phase and epicormic renewal phase but may enter phases of decline at various ages. 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

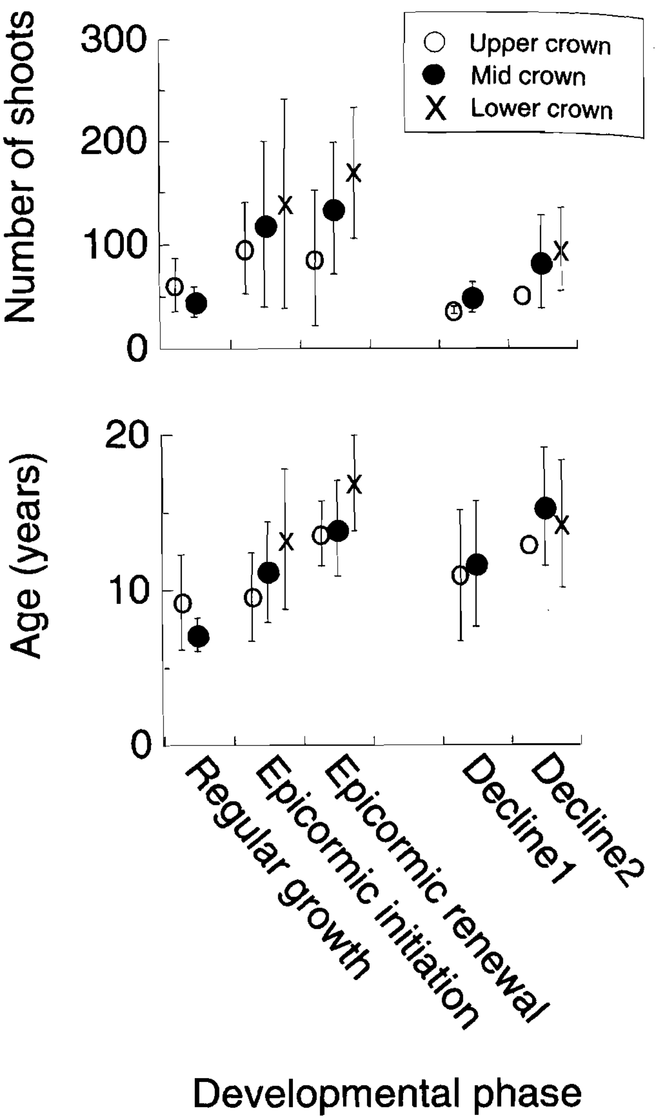
Fig. 6. Percentages of SCU of each branch in the various phases of SCU development for the tall, medium and short trees of *Pseudotsuga menziesii.*



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 or 4 years old (Fig. 8). The highest percentage of epicormic branchlets were produced when SCU were 6–13 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 or 7, 8 or 9, and 12 or 13 years, respectively.

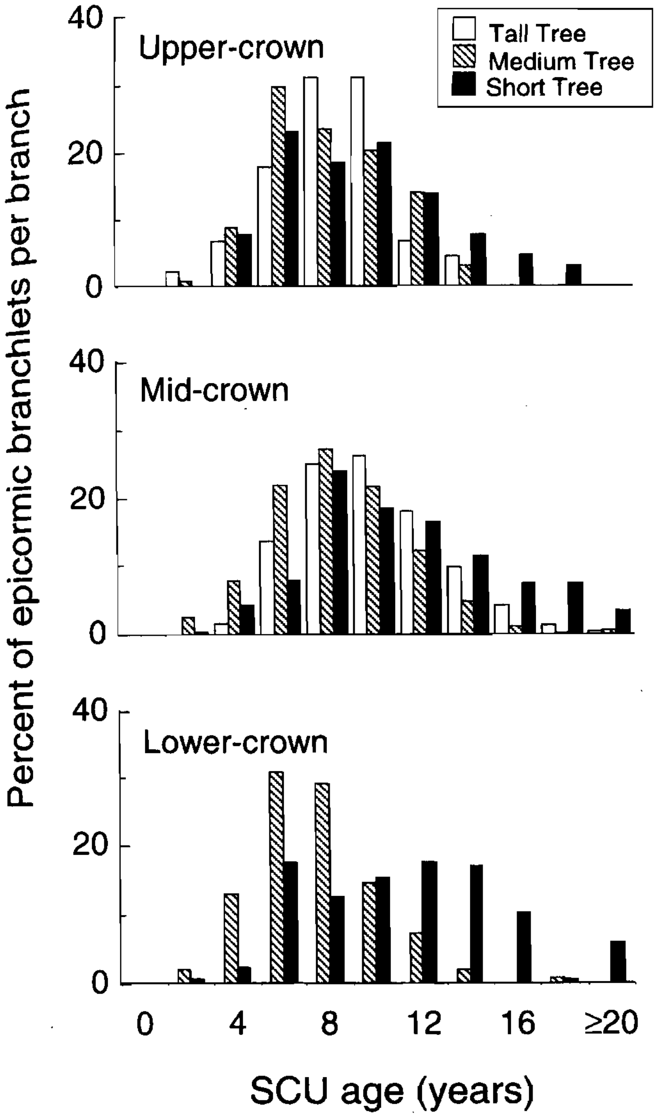
Fig. 7. Mean number of shoots and mean age of SCUs in various phases of SCU development for upper-, mid-, and lower-crown branches of the tall tree of *Pseudotsuga menziesii.* Error bars are ±1 SD. Only one SCU was observed in the decline 2 phase for the upper-crown branch; hence, there is no SD. No SCUs were observed in the regular growth phase and decline 1 phase for the lower-crown branch.



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 (Fig. 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 de-

Fig. 8. Frequency distributions of SCU age in *Pseudotsuga menziesii* when epicormic branchlets were produced, calculated by substracting the age of each epicormic branchlet from the SCU age. SCU ages are shown in 2-year age-classes.



creased 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 the 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 or 4 years old, and there was a peak to the production of epicormic branchlets at 6–13 years. Upper-crown branches produced epicormic branchlets at younger ages than did lower-crown branches, suggesting again 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 (Fig. 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). 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 of shoots (9.9%), foliage dry mass (7.0%), and foliage area (8.0%) produced by epicormic shoots, and the lower-crown branch had the highest percentage (49.8, 46.0, and 48.1% of shoots, foliage dry mass, and foliage area, respectively). For all branches, percentages of current-year shoots and foliage produced by epicormic shoots were higher than for all shoots combined, with ranges of 11.4–66.0% of current-year shoots, 8.1–64.6% of current-year foliage dry mass, and 9.4–48.1% of current-year foliage area.

The mode of the relative distribution of shoots, foliage dry mass, and foliage area across SCU age-classes increased

Fig. 9. Morphological characteristics of SCUs in various phases of SCU development for the mid-crown branch of the medium tree of *Pseudotsuga menziesii*. Bars show frequency distributions of regular lateral branchlets and epicormic branchlets along main axes of SCUs in 10-cm distance classes. Lines show percentages of regular and epicormic branchlets in each distance class that has live terminal buds.

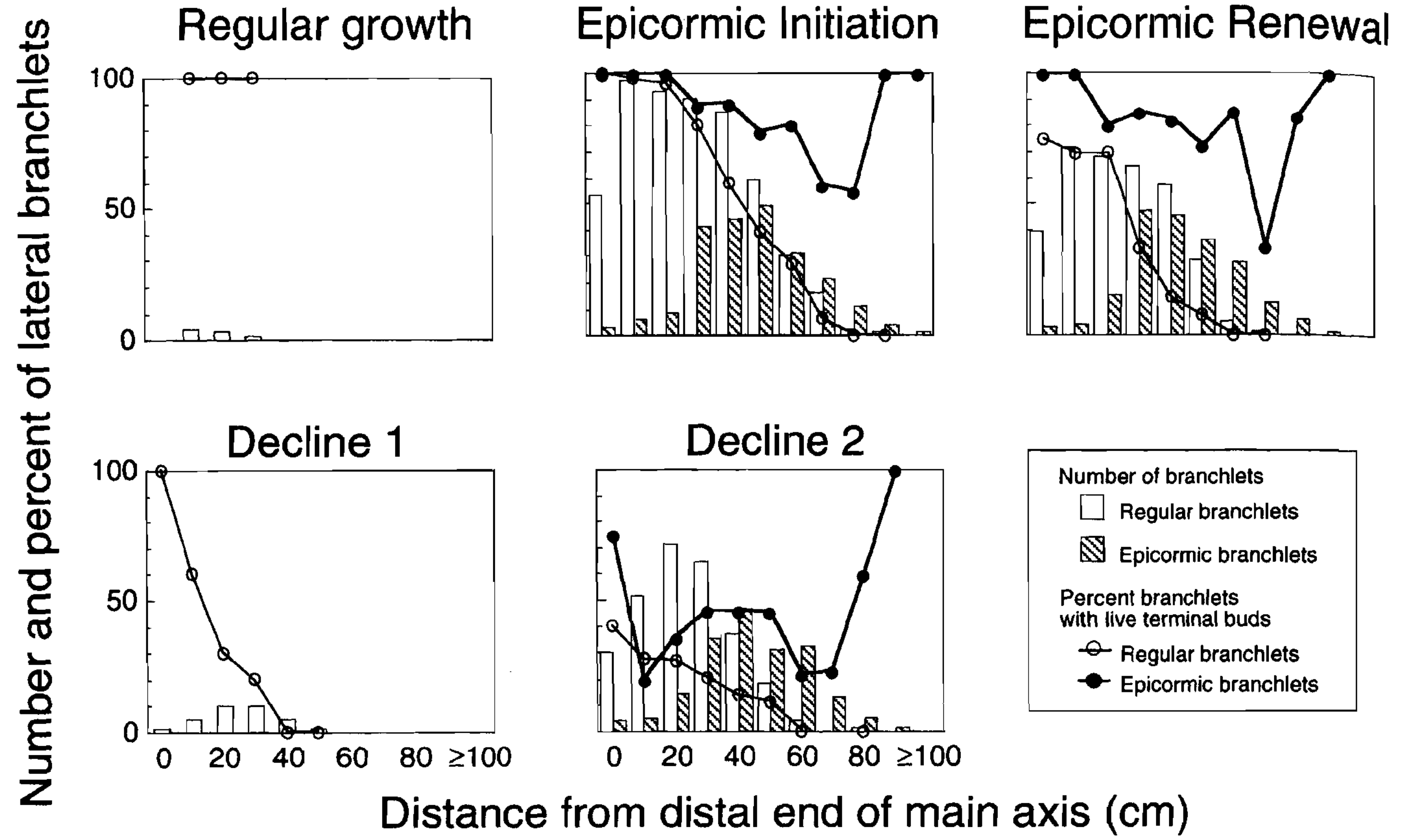


Table 3. Total amount of shoots, foliage dry mass, and foliage area of branches and percentages produced by epicormic shoots of *Pseudotsuga menziesii*.

Tree	No. of shoots		Foliage dry mass		Foliage area	
branch position	Total shoots	Epicormic (%)	Total (kg)	Epicormic (%)	Total (m²)	Epicormic (%)
Tall tree						
Upper crown	3 533 (1017)	9.9 (11.4)	1.000 (0.345)	7.0 (8.1)	4.235 (1.615)	8.0 (9.4)
Middle crown	13 577 (2108)	36.2 (50.4)	3.406 (0.625)	31.4 (54.2)	19.984 (4.599)	33.1 (46.6)
Lower crown	3 937 (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	6 284 (1304)	23.3 (30.3)	1.332 (0.334)	19.7 (27.5)	6.984 (1.953)	20.1 (27.2)
Middle crown	20 178 (3228)	32.2 (44.1)	4.020 (0.750)	25.1 (37.0)	25.752 (5.639)	26.0 (37.2)
Lower crown	6 533 (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	2 605 (583)	29.3 (35.6)	0.496 (0.119)	25.2 (32.4)	2.354 (0.727)	27.6 (34.6)
Middle crown	12 561 (1669)	19.7 (32.1)	2.316 (0.353)	16.6 (28.6)	13.892 (2.507)	17.4 (28.7)
Lower crown	4 112 (676)	38.6 (54.8)	0.584 (0.103)	33.0 (50.5)	3.942 (0.847)	33.7 (55.2)

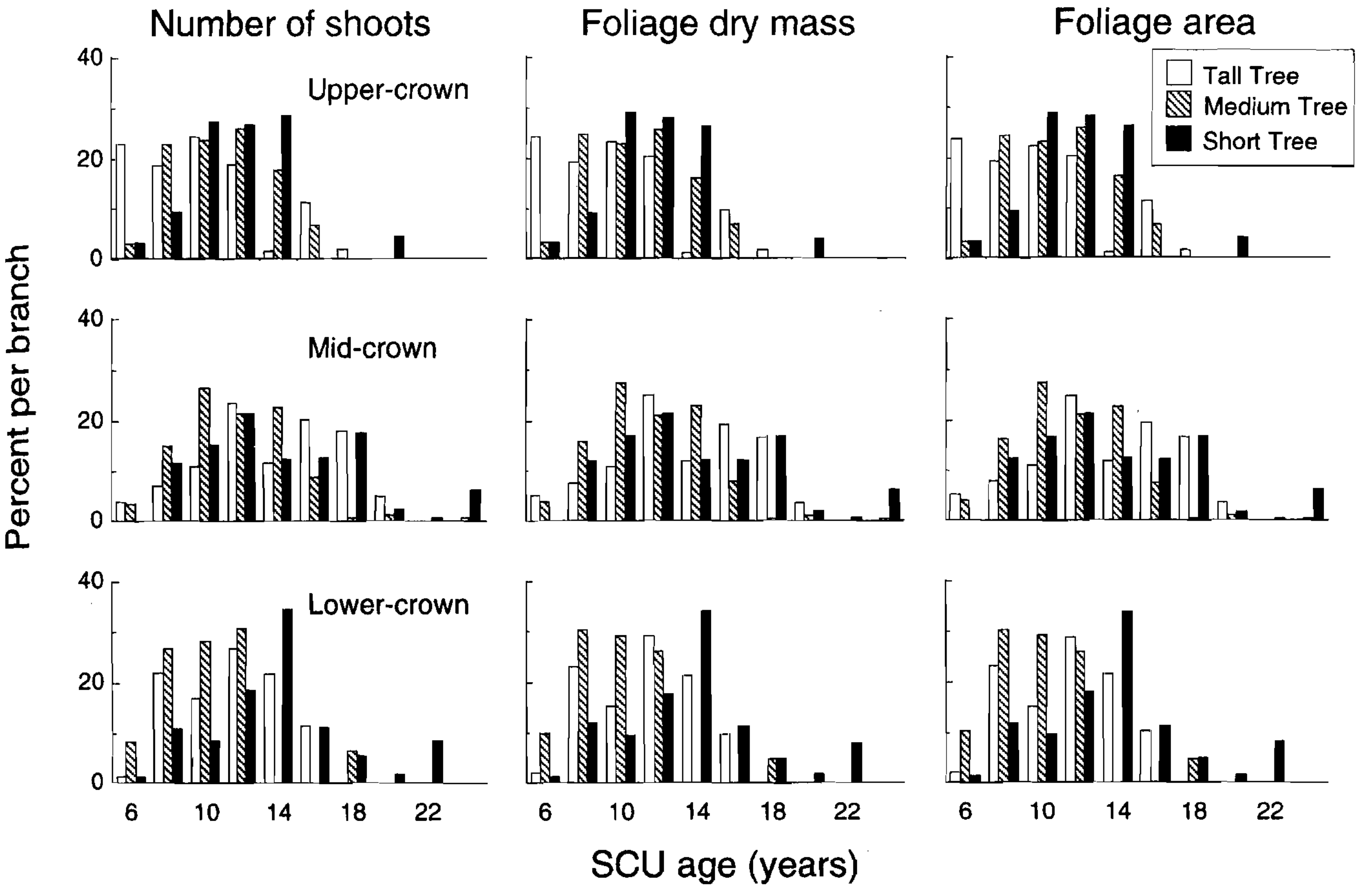
Note: Values in parentheses are the amount and percentages of current-year shoots and foliage.

from upper- to lower-crown branches (Fig. 10). This trend was strongest for the tall tree whose upper-crown branch had a mode at 10 or 11 years for number of shoots and 6 or 7 years for foliage dry mass and foliage area, while mid- and lower-crown branches had modes at 12 or 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, i.e., adaptive reiter-

Fig. 10. Percentages of shoots, foliage dry mass, and foliage area in each branch borne on SCUs of various ages of *Pseudotsuga menziesii*. SCU ages are shown in 2-year age-classes.



ation sensu Bégin and Filion (1999). Epicormic shoot production results in reiteration of SCUs and maintenance of shoots and foliage on branches of old *P. menziesii* trees.

Frequency and timing of epicormic shoot production

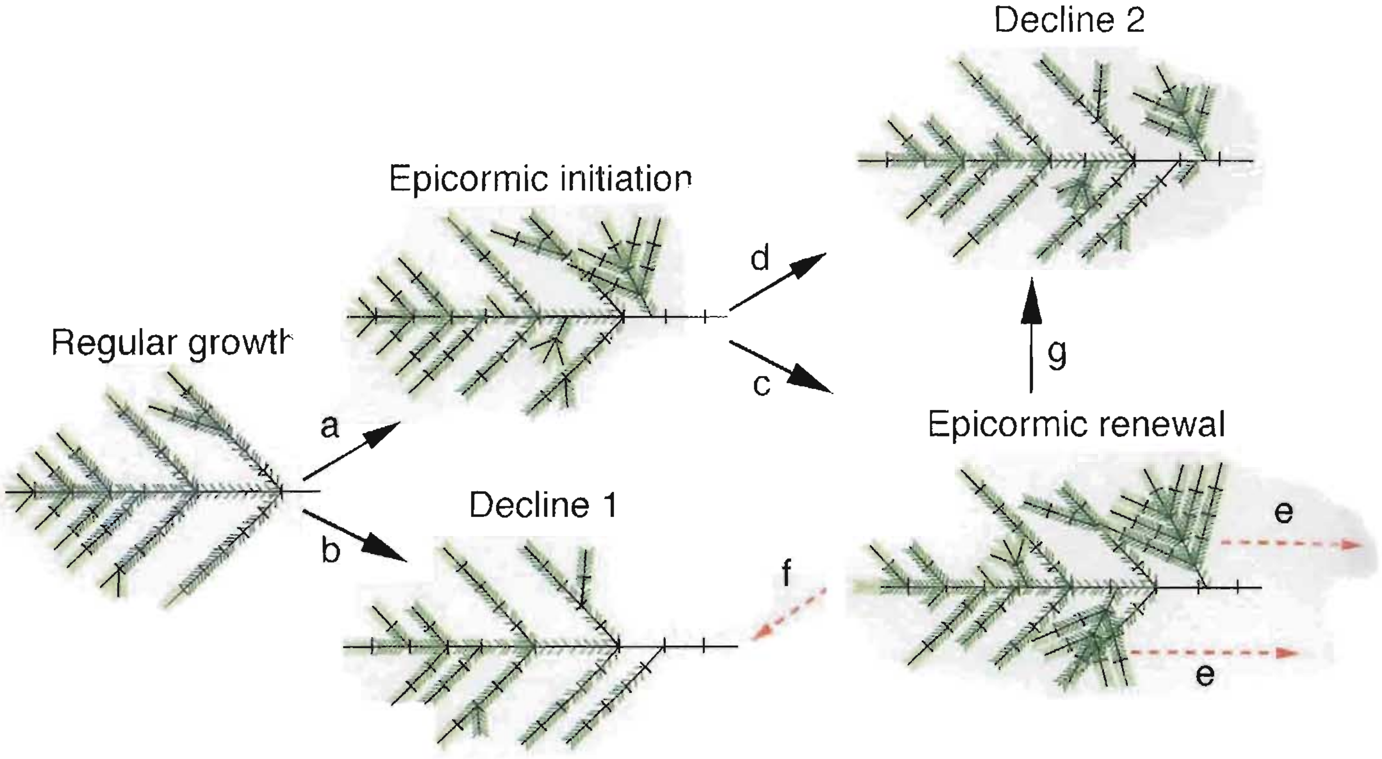
If epicormic shoot production were caused by exogenous stimuli such as damage, one would expect upper-crown branches, which are more exposed to harsh environments, to have a higher frequency of epicormic shoot production. However, frequency of epicormic shoot production was not higher for upper-crown 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 constantly and 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 frequency 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 suggest that release of epicormic buds from dormancy occurs constantly and 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 SCUs 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, had high percentages of SCUs in late phases of growth and reiteration, and had 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 because of the low-light environment of the lower crown, resulting in more frequent production of epicormic shoots and reiteration of SCUs.

Fig. 11. Schematic diagram showing the branching pattern and developmental phases of SCUs in *Pseudotsuga menziesii*. Light-green foliage denotes current-year shoots, while dark-green foliage denotes older shoots. Arrows (*a*–*g*) denote transitions between phases for the entire SCU (solid lines) and parts of SCUs (broken lines).



Figs. 12 and 13. Epicormic shoot production occurs at two larger scales in old *Pseudotsuga menziesii* trees. Three-dimensional forks (Fig. 12, arrows) form at the bases of sub-branch units reiterated by epicormic shoot production from older sections of the branch (branch diameter 18 cm). Epicormic branches (Fig. 13, EB) result from epicormic shoot production from the main stem and can be distinguished from original branches (OB, branch diameter 15 cm).

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 (Fig. 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 (Fig. 11*a*). SCUs begin producing epicormic branchlets as early as 3 or 4 years of age. The greatest number of epicormic branchlets are produced when SCUs were 6–13 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 (Fig. 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; Fig. 11*c*), or shoot production rates in both regular lateral branchlets and epicormic branchlets may decline (decline 2 phase; Fig. 11*d*). From the epicormic renewal phase, epicormic branchlets may grow further to form new SCUs that become independent of the parent SCU (Fig. 11*e*). The parent SCU may then be classified as being in decline 1 phase if no other epicormic branchlets are present (Fig. 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 (Fig. 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 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 young and mature *P. menziesii* (10–130 years old). We 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 reiteration of SCUs, we observed epicormic shoot production to occur at two larger scales in the crown of old *P. menziesii* trees. 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 (Fig. 12). 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 (Fig. 13). All three lower-crown branches in this study were epicormic branches. 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 stopped and contribute to prolonging individual tree life-span.

Acknowledgments

This research was funded by the Andrew W. Mellon Foundation, and conducted at the Wind River Canopy Crane Research Facility, a cooperative scientific venture among the University of Washington, USDA Forest Service Pacific Northwest Research Station, and Forest Service Gifford Pinchot National Forest. The authors thank Rebecca Bengtson, Hannah Chapin, Allison Cocke, Elaine Dinnie, Rebecca Douglas, Earthwatch ‘98, Steve Foster, Lindsey Horton, Kevin Hostert, Hyun-Seok Kim, Mayumi Kitade, Nate McDowell, the Oregon State University researchers, and Machiko Yamaguchi for their assistance. Thanks also to Sarah Greene, Annette Hamilton, and David Shaw for facilitating our study. Scientific input and helpful reviews of the manuscript were provided by Jerry Franklin, Tom Hinckley, Doug Sprugel, Marianne Turley, Craig Aumann, Dr. Chiristian Lacroix, and two anonymous reviewers.

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