Kobe University Repository : Kernel

PDF issue: 2025-12-05

Model analysis of the importance of reiteration for branch longevity in Pseudotsuga menziesii compared with Abies grandis

Ishii, Hiroaki
Kennedy, Maureen C.
Ford, E. David

(Citation)
Canadian Journal of Botany,82(7):892-909

(Issue Date)
2004-07

(Resource Type)
journal article

(Version)
Version of Record

(URL)
https://hdl.handle.net/20.500.14094/90000776

Model analysis of the importance of reiteration for branch longevity in *Pseudotsuga menziesii* compared with *Abies grandis*

Maureen C. Kennedy, E. David Ford, and Hiroaki Ishii

Abstract: Reiteration is an important process in the maintenance of tree crowns and in plant longevity. We use a geometric simulation model of branch growth to explore differences in longevity between old-growth *Pseudotsuga menziesii* (Mirb.) Franco and *Abies grandis* (D. Don ex Lamb.) Lindl. branches. Reiteration is defined through rules that reflect apical dominance relationships, and these rules are used to define shoot cluster units (SCU) on *P. menziesii* branches. Reiteration through epicormic production dominates growth in simulated *P. menziesii* branches and is shown to be a major factor that differentiates growth between *P. menziesii* and *A. grandis*. Branch growth is shown to be highly sensitive to rules for bifurcation and capacity for reiteration. The rules employed in the model that define epicormic initiation and SCU independence reveal possible physiological mechanisms through which reiteration occurs in *P. menziesii*. A simple morphological rule fails to simulate branch growth adequately, whereas a physiological rule through epicormic initiation after release from inhibition of a lateral axis yields realistic simulated branches. Branch growth is best simulated through a combination of physiological controls and morphological rules.

Key words: reiteration, old growth, architecture, branch modeling, longevity.

Résumé : La réitération est un processus important pour le maintient des houppiers des arbres et la longévité des plantes. Afin d'explorer les différences de longévité entre des branches de *Pseudotsuga menziesii* (Mirb.) Franco et de l'*Abies grandis* (D. Don ex Lamb.) Lindl. surannés, les auteurs ont utilisé un modèle géométrique de simulation de la croissance des arbres. La réitération est définie par des règles qui reflètent les relations de dominance apicale, et on utilise ces règles pour définir des unités de groupes de tiges (SCU) chez les rameaux du *P. menziesii*. La réitération par production épicormique domine la croissance chez les rameaux simulés du *P. menziesii*, et on montre qu'il s'agit d'un facteur majeur qui différencie les croissances du *P. menziesii* et de l'*A. grandis*. On montre également que la croissance raméale est très sensible aux règles qui régissent la bifurcation et la capacité de réitération. Les règles employées dans le modèle, définissant l'initiation épicormique et l'indépendance des SCU, révèlent des mécanismes physiologiques possibles par lesquels la réitération survient chez le *P. menziesii*. Une règle morphologique simple est impuissante à simuler adéquatement la croissance raméale, alors qu'une règle physiologique faisant intervenir une initiation épicormique, après le relâchement de l'inhibition imposée par l'axe latéral, conduit à des simulations réalistes des ramifications. On obtient la meilleure simulation des ramifications avec une combinaison de contrôles physiologiques et de règles morphologiques.

Mots clés : réitération, croissance surannée, architecture, modélisation de rameaux, longévité.

[Traduit par la Rédaction]

Introduction

An important advance in the understanding of tree longevity is the observation of reiteration through epicormic sprouting and description of the consequences this has on branch life-span. Begin and Filion (1999) found reiteration to be the main characteristic of young *Picea mariana* architecture and concluded that in the absence of reiteration a tree would rapidly suffer from dieback with the loss of foliage from its inner crown. Reiteration in the form of epicormic sprouting has also been observed in *Fraxinus pennsylvanica* (Remphrey and Davidson 1992) and *Pseudotsuga menziesii* (Mirb.) Franco (Bryan and Lanner 1981; Ishii and Ford 2001). Although epicormic sprouting can be induced by damage to branches (Bryan and Lanner 1981), Ishii and Ford (2001) stress that it occurs extensively in old-growth branches in the absence of obvious trauma.

Hallé et al. (1978) observe that reiteration of a basic architectural model is a fundamental morphological characteristic of tropical trees. Reiteration refers to growth that does not constitute the usual expression of the architectural

Received 8 January 2004. Published on the NRC Research Press Web site at http://canjbot.nrc.ca on 23 July 2004.

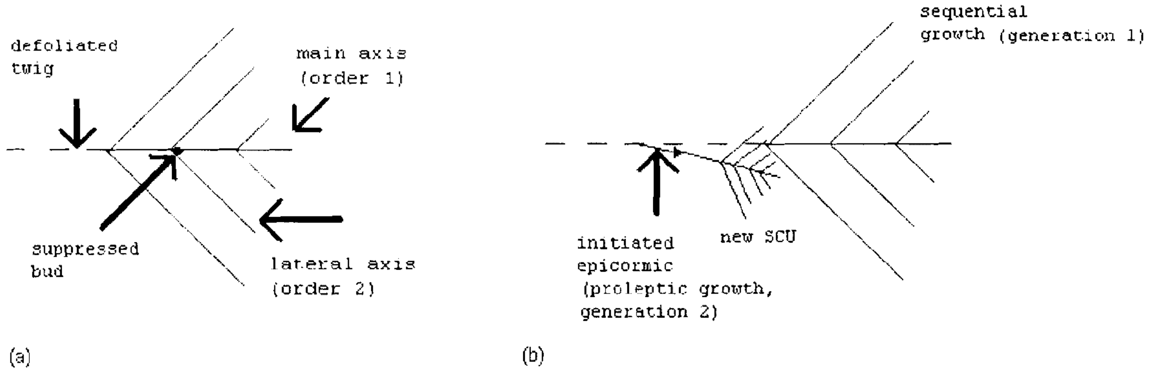
M.C. Kennedy.[1] Quantitative Ecology and Resource Management, University of Washington, Box 352100, Seattle, WA 98195-2100, USA.
E.D. Ford and H. Ishii.[2] College of Forest Resources, University of Washington, Box 352100, Seattle, WA 98195-2100, USA.

[1] Corresponding author (e-mail: mkenn@u.washington.edu).

[2] Present address: Division of Forest Resources, Graduate School of Science and Technology, Kobe University, Kobe 657-8501, Japan.

© 2004 NRC Canada

Fig. 1. Schematic of terms used, branches viewed from above. (*a*) In the diagram the main axis order 1 shoots have extension and two lateral shoots each year ($k = 3$), whereas lateral order 2 shoots only have extension each year ($k = 1$). Suppressed buds occur on order 1 shoots and can result in epicormic initiation. (*b*) If epicormic initiation is successful (indicated by the arrow at the base of the new shoot cluster unit (SCU)), proleptic reiteration of the main-axis structure results and generation increases. These generations can accumulate, and up to seven were observed in *Pseudotsuga menziesii* (Ishii and Ford 2001). The reiteration may or may not be of the same size as the original structure (it is shown smaller here to help distinguish it from the original structure). Sequential growth occurs as the original main and lateral axes extend each year. Sequential reiteration occurs when a lateral axis is given the same average bifurcation as the order 1 main axis (not shown).



model; rather, with the activation of an existing (often dormant) meristem, the complete replication of the original architectural model occurs. For tropical trees, Hallé et al. (1978) report this as miniature tree forms extending vertically from lateral branches, repeating the model of growth observed on the main stem of the tree, similarly observed by Edelstein and Ford (2002) in *Thuja plicata*. Ishii and Ford (2001) observed shoot cluster units (SCU), morphologically distinct plagiotropic clusters of foliage in *P. menziesii* (Ishii and Ford 2001, their Fig. 3), which are formed through proleptic reiteration and occur horizontally on existing branches.

The basic architectural model of branch growth in old *P. menziesii* is a main axis of the branch (the first order directly off the main trunk) that has two or three daughter shoots per year, with lateral axes that produce one or two daughter shoots per year (Fig. 1). We consider this to be an expression of apical dominance of the terminal apex of the branch clusters on the lateral axes, limiting whether their buds form shoots (see Ford 1985; Cline 1994; Wilson 2000), whereas the shorter growth of shoots from buds on lateral axes that do grow is an expression of branch apical control. The proleptic growth of epicormic shoots observed by Ishii and Ford (2001) involves formation of a bud that remains dormant at the same node on the main axis as lateral branches and is usually in the adaxial position. Wilson (2000) restricts the term "apical dominance" to describe the control of the outgrowth of a meristem the year it is formed and does not apply it to any form of proleptic growth. In the current paper, we use apical dominance to describe the suppression of bud outgrowth, regardless of how long ago the bud was formed (for further discussion of apical dominance see Wilson 2000; Cline and Sadeski 2002). In epicormic growth, a suppressed bud can be released from the dominance of its terminal apex (on average 5 years later) and sprout, which we define to form a higher generation of shoot growth (Fig. 1). Thereafter its growth repeats the basic architectural model of the main branch axis. These repetitions form the SCUs, which are deemed morphologically distinct from the parent axis if the SCU is separated spatially because of death of needles at its base (Fig. 1; Ishii and Ford 2001, their Fig. 3). Using this morphological criterion, Ishii and Ford (2001) observed up to seven epicormic generations (Fig. 1) that resulted in SCUs on *P. menziesii* branches. They also discerned five phases in the growth and decay of an SCU (Ishii and Ford 2001, their Fig. 11). Ishii and Ford (2001) propose reiteration as an explanation for how *P. menziesii* can be a long-lived pioneer, that is, establish after a major disturbance, yet persist in the upper canopy throughout forest succession.

This paper explores the following overarching question: What branching characteristics facilitate the perseverance of *P. menziesii* in the forest canopy through all stages of forest development? To provide context in the study of *P. menziesii*, *Abies grandis* (D. Don ex Lamb.) Lindl. branching was also analyzed. *Abies grandis* coexists with *P. menziesii* in such old-growth forests, but it does not grow as tall nor live as long, and the contribution of epicormics to growth in *A. grandis* is negligible. In the context of the conclusions drawn by Ishii and Ford (2001), two morphological and ecological questions emerge:

(1) How does epicormic sprouting result in morphologically distinct and repetitive clusters of foliage throughout the *P. menziesii* branching structure? The SCU, as described by Ishii and Ford (2001), has the morphological characteristic of lack of continuity of live foliage. Does it also have a physiological origin because of release from the apical dominance of an existing branch axis, which allows the bud to grow, accompanied by the establishment of similar control within the SCU (physiological independence)? If not, then the division of a branch into SCUs may be an artifact of the morphological characteristics of the branch. For example, in *A. grandis* sequential lateral axes have relatively high average bifurcation

© 2004 NRC Canada

and visually resemble the characteristic main axis we have described for *P. menziesii.* Do these constitute SCUs as well?

(2) What are the advantages of repetitions of architectural structure throughout a branching system? Ishii and Ford (2001) stress that proleptic reiteration allows *P. menziesii* to maintain foliage throughout its crown when limitations of crown width prevent much foliage production at the terminal ends of branches (Ishii and Wilson 2001). How effective is proleptic reiteration in compensating for such size limitations?

To answer the first question, the description of the SCU provided by Ishii and Ford (2001) was used to organize foliage in simulated branches of both *A. grandis* and *P. menziesii.* In this paper, SCUs are considered organizational units if their reiterative properties (acting as a first-order main axis and thereby being considered physiologically independent) can be applied to all such groupings throughout the branch, regardless of location. To answer the second question, we use the comparison between *A. grandis* and *P. menziesii.* We surmise that *A. grandis* is able to maintain its live crown through a concentration of tightly packed foliage located distally on branches and a higher branch density through its crown (number of branches per metre height growth; H. Ishii and D.C. Shaw, unpublished data), whereas *P. menziesii* has a more sprawling branching structure, with foliage maintained proximally along the branching axis (see Ishii and Wilson 2001 for branching density of *P. menziesii*). To explore both questions, we developed and assessed a computer simulation model of branch growth. In a computer simulation we can explore the effect of adjusting parameters of growth, manipulations that are difficult or impossible in the field. With computer simulations we can also observe the development of the branch structure through the entire course of development, rather than inferring development from a cross-sectional study of branch structures of different ages (for examples of plant models see Honda 1971; Honda and Fisher 1978; Franco 1986; Sutherland and Stillman 1988; Ford et al. 1990; Sorrenson-Cothern et al. 1993). We developed a stochastic model that accommodates reiteration, where reiteration occurs on existing branching structures. We do not simulate the reiteration of new leaders or new branches produced on the main trunk. The model is designed to simulate growth for the potential life-span of the branch for both *P. menziesii* and *A. grandis.*

Methods

Data collection and analysis

Data for *P. menziesii* were obtained from Ishii (2000) and used to generate regression relationships for both foliage mass and area predicted by foliage age and order. New data were gathered for *A. grandis* (Kennedy 2002) in the same manner as Ishii (2000), with the exception that only three total branches were harvested and measured because of limitations to sampling in the Forest Service old-growth Natural Research Area: one branch was harvested from the lower crown, one from the middle crown, and one from the upper crown of three different trees. These data were used to produce regression relationships for *A. grandis* to predict foliage mass and area. Additional nondestructive measurements of architectural branching characteristics, including lateral branching angle and the ratio of lengths between parent and lateral shoots for both *P. menziesii* and *A. grandis,* were made at the Wind River Canopy Crane Research Facility (WRCCRF). The growth of young epicormic shoot structures was also measured: the length and age of daughter shoots of the initiated epicormic and the number of daughter shoots per node was recorded for five clusters on each measured branch. Maps of these newly forming clusters reveal limited growth for the first 2 years, then increasing growth thereafter both in the bifurcation of the epicormic axis and in the average length of shoots (Fig. 2).

Construction of the simulation model

Terms: shoot order and generation

Shoots are ordered according to the botanical ordering system (Borchert and Slade 1981), which assumes functional relationships among the shoots in the branching systems (Uylings et al. 1975). Shoots that come directly from the trunk are ordered one; lateral shoots are assigned an order one greater than their parent, and shoots that represent extension of the parent axis are the same order as the parent (Fig. 1). Sequential growth is growth within the usual timing of the tree (after a single winter of dormancy), and proleptic growth is growth from a bud that has been dormant for more than one winter. Similarly, sequential reiteration is the dedifferentiation of a lateral apex to function as a first-order main axis within the usual timing of growth, and proleptic reiteration is the release from dormancy of an epicormic shoot, which then reiterates the structure of the main axis (Fig. 1). All epicormic shoots are assigned to order 1 (so that they reiterate the structure of the branch main axis), and the main axis of any independent SCU is assumed to be order 1.

Generations are assigned to distinguish the growth of epicormic shoots from regular lateral shoots. The first shoots grown in the simulation are assigned to generation one, and all shoots produced through sequential growth are the same generation as their parent. An epicormic sprout is assigned to a generation one greater than that of its parent (Fig. 1, Ishii and Ford 2001).

Model structure

Much of the language for the two-dimensional model follows Ford and Ford (1990) and Ford et al. (1990). The simulation model runs on a yearly time step and performs the following functions each year:

(1) Regular shoot growth: New shoots are produced at the terminal end of active nodes and are assigned predicted lengths, foliage masses, and areas.

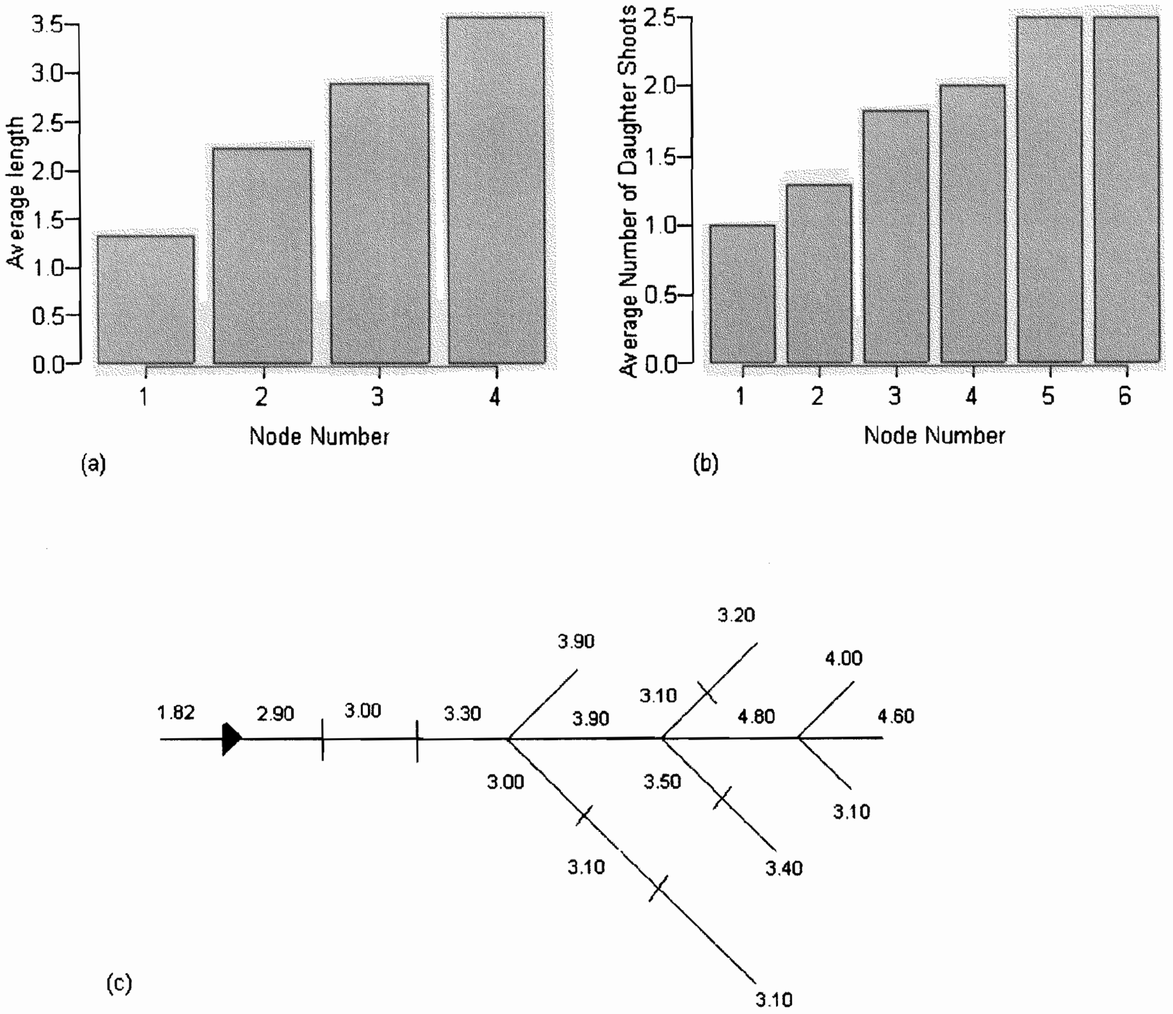
(2) Epicormic initiation: The model tests whether previously suppressed buds are due to be released from inhibition.

(3) SCU independence: If a collection of shoots satisfies the criterion to become a newly independent SCU, then that collection of shoots is considered to form a new SCU distinct from the parent axis.

Model parameters

The six model parameters are values important for growth that are used in the model but were not determined through

Fig. 2. Growth of a newly forming shoot cluster unit (SCU) in *Pseudotsuga menziesii*. (*a*) The average length of internodes increases from the base of the new SCU outward (node number is the sequence of shoots, where node number 1 is the first shoot at the base of the newly forming SCU, node 2 is the main-axis daughter of node 1, etc. There are data only for the first four nodes) (*b*) The average number of daughter shoots also increases from the base of the SCU out along its main axis (six nodes measured). (*c*) Map of a typical young epicormic shoot in *P. menziesii*, demonstrating limited growth and expansion during the first few years, then exhibiting the characteristics of SCU growth between years three and four. In the simulation the average bifurcation the first 2 years of epicormic growth is assumed to decrease with increasing generation. The arrow represents the newly initiated epicormic shoot and differentiates it from a sequential lateral axis. Numbers are shoot length (cm); map not to scale.



observation or were of particular interest to explore (Table 1). The continuous parameters are bifurcation ratios for shoots of different orders. The other two parameters are different rules of growth: three alternative rules for epicormic initiation and two alternative rules for SCU independence.

Bifurcation ratios

Kull et al. (1999) model the probability of a shoot forming k new shoots as a Poisson process, with the rate parameter equal to the average bifurcation ratio (λ):

$$[1] \quad P(k) = \frac{\lambda^k e^{-\lambda}}{k!}$$

For each newly grown shoot, a number k is drawn from a Poisson distribution, with a bifurcation ratio as the rate parameter. The value k represents the number of buds formed the previous year that will elongate into shoots. This is a desirable formulation because the parameter of the Poisson distribution (bifurcation, average number of daughter shoots per year) has a biologically meaningful interpretation, and there is a lack of understanding of the fates of buds (e.g., Maillette 1982). The algorithm for this random number generation was taken from Press et al. (1992). Priority in growth is given to extension of the shoot. For example, if $k = 1$, then there is only extension the next year. If $k = 2$, then there is extension and one lateral shoot each year (Fig. 1*a*). In the model, the most daughter shoots allowed at each node is 3. In general, that is the case observed in the old-growth species, and this limitation simplified the simulations. The Poisson distribution yields any integer value zero and greater, so in the model any shoots that draw a number

© 2004 NRC Canada

Fig. 3. Plots of total foliated shoots over time for *Abies grandis* with 50 runs at the same parameter values. (*a*) In the initial model where all orders greater than 3 are given the same average bifurcation as order 3, there is unrealistically high maximum numbers of foliated shoots. (*b*) When a reduction in bifurcation occurs with order >3, the range of the number of foliated shoots is greatly reduced.

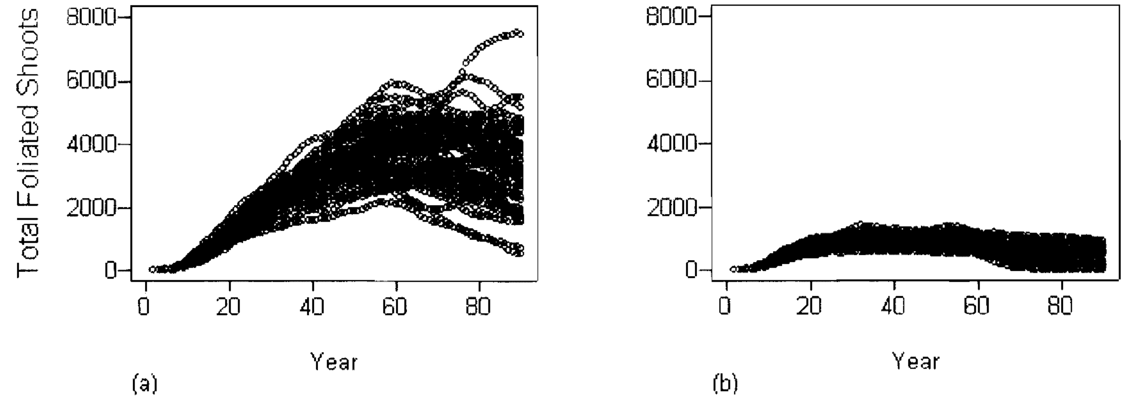


Table 1. Parameters used in the simulation model.

			Default values	
Parameter	Definition	Possible values	*Pseudotsuga menziesii*	*Abies grandis*
rba	Average bifurcation of first-order shoots	(0,4)	2.5	3
rbb	Average bifurcation of second-order shoots	(0,4)	1.5	2
rbc	Average bifurcation of third-order shoots	(0,4)	0.5	1
epirba	Average bifurcation of newly initiated epicormic shoots	(0,4)	0.7	na
rule	Designates which of two rules will be applied for SCU independence	0 or 2	0	0
eprule	Designates which of three rules will be applied for epicormic initiation	0, 1, or 2	1	1

Note: na, not applicable.

greater than 3 are assigned three daughter shoots. This changes the probability of drawing a three as follows:

$$[2] \quad \begin{aligned} P(k=3) &= P(k \geq 3) \\ &= 1 - P(k = 0, 1, \text{ or } 2) \\ &= 1 - \sum_{i=0}^{2} \frac{\lambda^i e^{-\lambda}}{i!} \end{aligned}$$

where the mean of the distribution is no longer exactly the λ parameter. For example, if the value for average bifurcation is 3.0, the actual mean number of daughter shoots will be 2.328. Any bifurcations explored must therefore be considered in the context of this reduced expected value. There are unique parameters for the average bifurcation of order 1 (rba), order 2 (rbb), order 3 (rbc) and new epicormic shoots for the first 2 years (epirba), and default values for the parameters that were determined through initial simulations (Table 1).

It is the general case for these species that average bifurcation decreases with increasing order. If bifurcations of shoots ordered greater than 3 are simply given the order 3 parameter value, there are unrealistically high values of total shoots at year 90 for *A. grandis* simulations, with significant variability (Fig. 3*a*). To prevent the requirement for a unique parameter for all possible shoot orders greater than 3 a simple monotone negative relationship was used for the average bifurcation of all shoots greater than order 3:

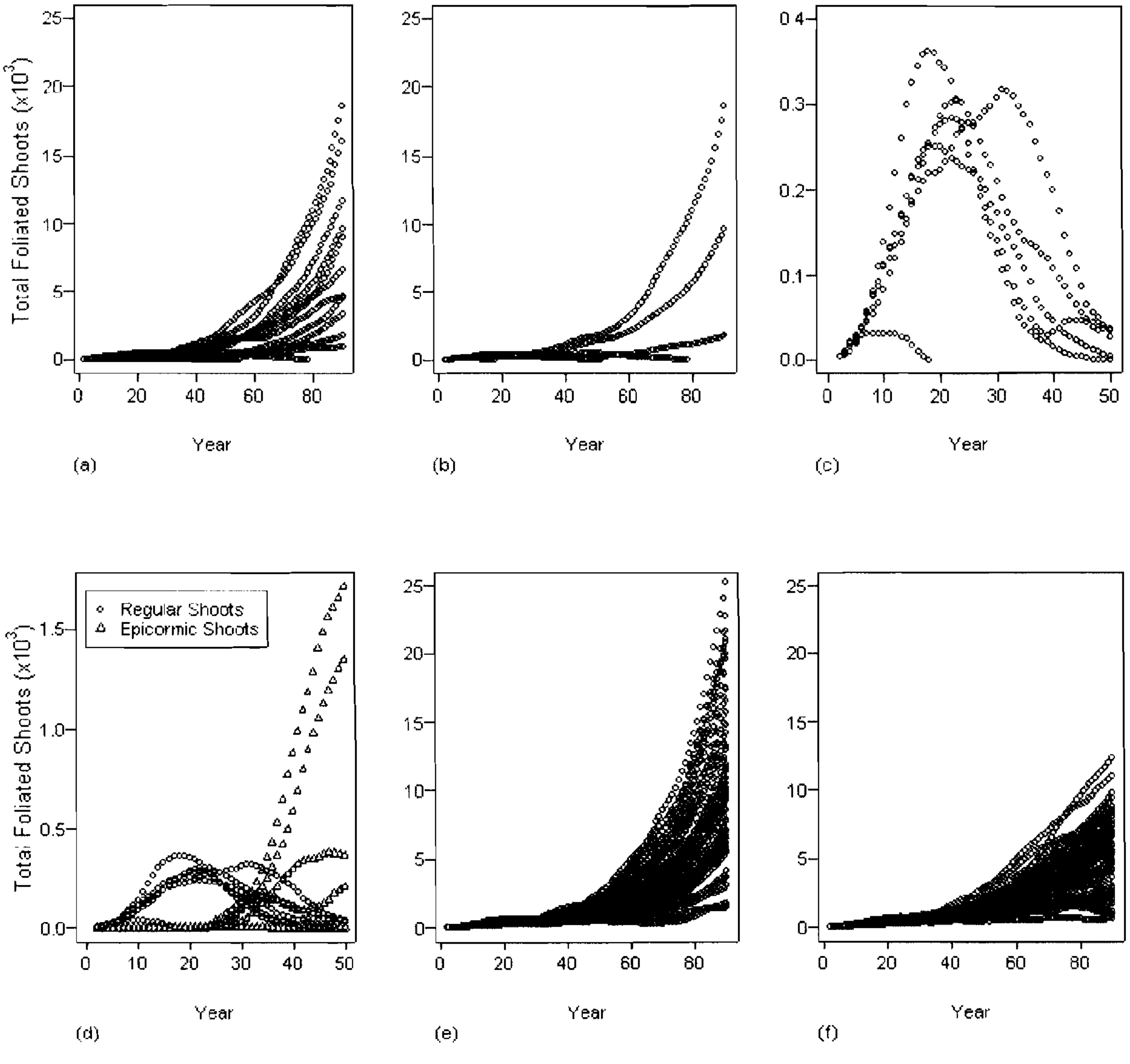
$$[3] \quad \mathrm{Rb}_{>3,\mathrm{red}} = \mathrm{Rb}_3 \times \frac{3}{\mathrm{shoot}_{\mathrm{order}}}$$

This reduction successfully reduced the range and variability of total simulated shoots at year 90 for *A. grandis* (Fig. 3*b*).

Initial simulations also demonstrated strong cumulative effects of epicormic growth on the outcome of simulations. For *P. menziesii* many initial simulated branches did not survive until the minimum age observed by Ishii and Ford (2001; Table 4), and for the simulated branches that persisted the outcomes were highly variable (Figs. 4*a*, 4*b*). Some simulated branches had more than three times the total foliated shoots that were observed by Ishii and Ford (2001). Our goal was to observe long-term branch development, and it seems necessary to enforce a minimum amount of growth to prevent the premature death of a simulated branch. The model was thereby modified to allocate deterministically three daughter shoots each year to the terminal node of the regular main axis for the first 50 years of sequential growth ($\mathrm{rand}_{\mathrm{main}}$ = 50). Thereafter the regular main axis becomes subject to the random Poisson process.

Initial simulations also showed that reiteration had significant cumulative effects on the number of foliated shoots on

Fig. 4. Plots of total foliated shoots over time for *Pseudotsuga menziesii*, where each curve represents a single run. (*a*) There is an unrealistically high number of shoots in the initial model, without any reduction in epicormic initiation with increasing generation, with 50 runs at the same parameter values. (*b*) Foliated shoots for six seed values chosen for detailed analysis. (*c*) Regular shoots for the six seed values show similar growth over time. (*d*) Divergence of growth among the six seed values is evident in the course of epicormic shoots over time, indicating that differential success of reiteration early in growth explains the variability observed in branch development and the significant cumulative effects of reiteration. (*e*) A deterministic main axis results in positive and variable growth for 50 runs. (*f*) A reduction in growth with increasing epicormic generation (eq. 4) restricts the upper range of total shoots for 50 runs.



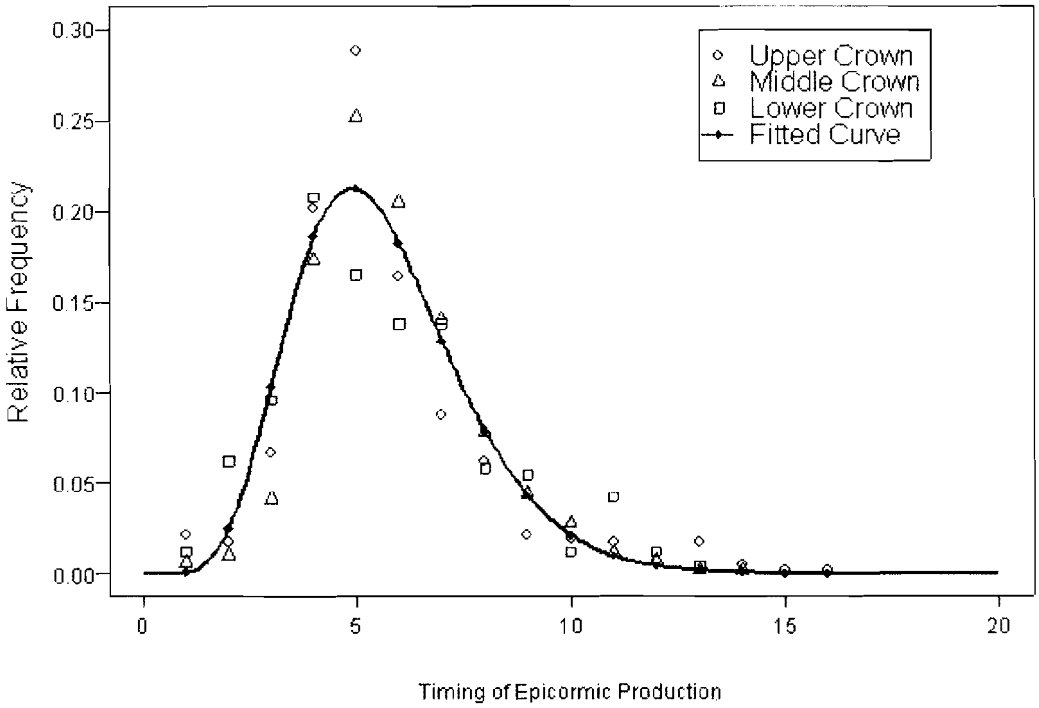
the branch (Figs. 4*c*, 4*d*), resulting in simulated branches with foliated shoots more than three times the maximum observed (Fig. 4*e*, Table 4; Ishii and Ford 2001). To prevent the shoot development from reiteration to produce impossibly large branches it was found necessary to decrease the probability that a newly sprouted epicormic shoot bifurcates successfully. Hallé et al. (1978) observed a decrease in both the size and the number of branches and internodes of reiterative complexes of tropical species as the number of complexes increased. The method used to accomplish a decreased success of initiation was an inverse relationship between bifurcation of new epicormic shoots and generation above a chosen generation ($\mathrm{gen_{red}}$):

$$[4] \qquad \mathrm{Rb_{ini,red}} = \mathrm{Rb_{ini}} \times \frac{\mathrm{gen_{red}}}{\mathrm{epi_{gen}}}$$

A value of three for $\mathrm{gen_{red}}$ yielded reasonable simulated branches (Fig. 4*f*), and that was chosen as the default value. This equation is then applied for all epicormics with a gen-

© 2004 NRC Canada

Fig. 5. Distribution of the timing of epicormic production (data from Ishii (2000)). The distributions of relative frequency of timing of epicormic production show similar shapes at all three crown positions, and a gamma distribution was chosen that approximates the shape of the frequency distribution. The probability of epicormic initiation peaks around age five and declines thereafter.



eration of four and above. This reduction only applies to Rb_{ini}, that is, to the first 2 years of growth for a new epicormic, such that if the initiated shoot successfully elongates subsequent growth proceeds regardless of generation. This reduction restricts the probability that a new epicormic shoot successfully develops into an SCU for higher generations and restricts baseline model outcomes closer to the range observed (Fig. 4*f*, Table 4).

Rules for epicormic initiation

Ishii (2000) recorded the timing of epicormic initiation, that is, the number of years of dormancy before a bud sprouted into an epicormic shoot. Analysis of his data shows that the timing of epicormic initiation (Fig. 5) peaks around 5 years after the bud is formed and then declines. The asymmetric shape of this distribution resembles the gamma probability distribution (Casella and Berger 1990), which is the sum of exponential distributions. The exponential distribution is a waiting-time distribution, and this can reasonably be interpreted as the waiting time to epicormic initiation. This distribution as a modification of the exponential may reflect that it is not inevitable that a dormant bud sprouts to form an epicormic shoot. For the simulations we assume that the gamma density is an appropriate statistical model for timing of epicormic initiation in *P. menziesii*. As such, the age at which that shoot may sprout an epicormic is generated from the gamma distribution for each newly grown first-order shoot (Press et al. 1992). For example, if a parent shoot draws the number five, then the shoot is tested for epicormic initiation during the time step at which it is 5 years old. Parameters were chosen that qualitatively produced a gamma probability distribution that matched the observed values and had a similar mean (α = 8, β = 0.7; Fig. 5). Although these parameters do not have biological interpretations, the gamma distribution defined by them closely resembles the observed distribution (Fig. 5).

Once the shoot reaches the age that was drawn for it from the gamma distribution, and if the shoot satisfies the criterion for epicormic initiation under which the model is running (see below), then an epicormic shoot is produced. If not, the bud is aborted. Epicormics are simulated to sprout only on existing branching structures. The measured rate of epicormic initiation in *A. grandis* was too infrequent to be similarly analyzed, and epicormics are assumed to have a negligible effect on *A. grandis* growth. It must be noted here that the data for the timing of epicormic initiation were gathered for epicormic shoots that had already sprouted and excluded any nodes that did not successfully sprout epicormics. Therefore, the probability of sprouting at a particular year is likely overestimated, which is compensated for in the alternative rules for epicormic initiation.

These rules were developed under the assumption that apical dominance operates to establish a clear main axis on branches in *P. menziesii*, but some mechanism of release from apical dominance is required in the process of epicormic sprouting to enable reiteration. It is reasonable that a laterally growing axis producing auxin may contribute to maintaining dormancy of epicormic buds, which can be released when the lateral apex is lost. This idea is explored in the three alternative rules for epicormic initiation (Table 1):

(1) Simple initiation: Under this rule there are no further restrictions on epicormic growth and a shoot produces an

© 2004 NRC Canada

Table 2. Constants used in the simulation model.

Constant	Description	Possible values	Units	Explanatory variables	
				Pseudotsuga menziesii	*Abies grandis*
theta	Lateral shoot branching angle	(±) (0,π/2)	rad	Parent length	Parent order, parent length, crown position
lrat	Length ratio between shoots of different orders	(0,1)	Unitless	Parent order, crown position	Parent order, crown position
sna	Specific needle area: ratio of foliage area to foliage dry mass	(0,∞)	cm^2/g	Shoot age, SCU position, crown position	Shoot age, SCU position, crown position
ma.l	Mass per length: the foliage dry mass predicted for a given shoot length	(0,∞)	g/cm	Shoot age, crown position	Shoot age, crown position
length	The initial length and subsequent lengths of first-order shoots	(0,10)	cm	None	None

Note: SCU, shoot cluster unit.

epicormic when it reaches its designated timing. This assumes some mechanism other than lateral suppression of the dormant bud.

(2) One inactive side: A possible theory for the release of dormant buds is the requirement that at least one of the lateral axes that is subtended from the same node as the suppressed bud is no longer growing. If both the lateral shoots are still active at the designated time, then the lateral axes are assumed to be suppressing the dormant bud, which is then aborted.

(3) Two inactive sides: In this case both of the lateral subtended axes must no longer be growing in order for the bud to sprout an epicormic, giving a stricter form of apical dominance of the lateral shoots on the suppressed bud, that is, if one axis is still growing the dormant bud remains suppressed.

Under all three rules, epicormics sprout only on order 1 axes and after the first 2 years of growth the epicormic axis is given the same average bifurcation as other first-order shoots.

Rules for defining SCU independence

Each year the model searches for groups of foliage that are recognized as newly independent SCUs, and each shoot in the group is then assigned an SCU number. Two criteria to distinguish independent SCUs can be discerned from the theory of Ishii and Ford (2001):

(1) Contiguity rule: An SCU is considered independent of the parent unit if it has formed a "petiole-like section separating its shoots spatially from the parent SCU" (Ishii 2000). Under this rule, a lateral axis or epicormic is assumed independent of the main axis when foliage mortality occurs at its base, resulting in lack of contiguity of foliated shoots with the main axis. The shoots on the main axis of the new SCU are given order 1; the remaining shoots are reordered accordingly. This rule relies solely on the morphologically distinct characteristic of the observed SCUs.

(2) Epicormic rule: Only epicormic shoots form the basis of a new SCU, which is assumed to be independent if it is older than 10 years. This preserves the contiguity criterion for epicormic shoots described above, but lateral shoots are never considered to be independent SCUs, because they do not bifurcate as first-order axes. This gives a stronger physiological basis for independence.

For both rules there is a minimum of 10 shoots that can comprise an independent SCU, so the axis has grown at least longer than the maximum assumed foliage longevity. If the structure has fewer than 10 shoots, it is labeled as "miscellaneous".

Model constants

Regressions obtained through data analysis were used in the model to determine foliage amounts for a shoot of a given age and location for both species (Table 2). When the statistical relationship predicted less than zero foliage mass and area, or if the shoot was older than the maximum age observed (10 years), the shoot was considered defoliated. Regression equations were also generated for architectural parameters, including branching angle, and the ratio of lengths between parent and daughter shoots of different order (Table 2). For simplicity, a shoot that is the extension of the parent is assumed to have the same length as the parent (i.e., constant growth rate along an axis of particular order).

Sensitivity analysis

For each species a local sensitivity analysis (Campolongo et al. 2000) was performed for values of average bifurcations in conjunction with factor screening of the different rules for independence of SCUs (two rules) and epicormic initiation (three rules). In this model the two factors (SCU independence rules and epicormic initiation rules) have six distinct combinations (Table 3), and the local sensitivity analysis was repeated for each of the six rule combinations (see below). For *A. grandis* the three different rules for epicormic initiation were not explored because epicormics were assumed to make a negligible contribution to growth.

For sensitivity analysis 80 unique parameterizations were generated for each rule combination. Each continuous parameter was sampled 20 times from a uniform distribution, with the others kept at their default values. For *P. menziesii* the parameters were sampled on the range (0,3), and for *A. grandis* the parameters were sampled on the range (0,4). There are strong stochastic effects in the model (Fig. 4*f*), and to try to control for them in the sensitivity analysis a single random seed was used for each parameter set. Two runs with the same parameter values would therefore result in identical branches. A random seed integer that yielded a central value in a population of 50 model outputs was chosen for use throughout the sensitivity analysis (seed = 21 and

© 2004 NRC Canada

Table 3. Rule combinations used for sensitivity analyses.

Rule combination	Description
1	SCUs develop on both lateral and epicormic axes; epicormics sprout only if one lateral axis is inactive
2	SCUs develop on both lateral and epicormic axes; no limitation on epicormic initiation
3	SCUs develop on both lateral and epicormic axes; epicormics sprout only both of the lateral axes are inactive
4	SCUs develop solely on epicormic axes; no limitation on epicormic initiation
5 (default combination)	SCUs develop solely on epicormic axes; epicormics sprout only if one lateral axis is inactive
6	SCUs develop solely on epicormic axes; epicormics sprout only if both of the lateral axes are inactive

Note: SCU, shoot cluster unit.

17 for *P. menziesii* and *A. grandis*, respectively). Analyses were repeated for each species, and to save computation time the model was run for 90 years for both species (Y90). This year was chosen as a central branch age observed in *P. menziesii*, although no *A. grandis* branches were observed at that age. Total foliated shoots at Y90 was plotted against the sampled bifurcation ratio to infer the effect of increasing bifurcation at each branch order on shoot growth.

Analysis of branch longevity

In addition to sensitivity analysis, model behavior was observed for up to 400 years at the default parameter values for each species. If the branch terminated before 400 years, the simulation ended, and the corresponding year was recorded as the terminal age of the branch. The total foliated shoots over time was observed for branches that were generated from five simulations at default parameter values for each species to assess variability in the long-term pattern of growth. In addition, a population of 50 branches was produced for both species, and frequency histograms of terminal age of the branch were plotted. For *P. menziesii* the total SCUs over time and the number of sequential and epicormic shoots per SCU over time were plotted for a single simulation. The development of a single SCU in *P. menziesii* was observed through frequency histograms of shoots of different age-classes over time.

For *P. menziesii* the epicormic generation at which reduced epicormic growth was applied in the simulation (gen_{red}, eq. 4) was explored through analysis of 50 simulations that were produced for each gen_{red} ranging from one to seven, with all other parameters at their default values. The terminal year of the branch and the maximum number of foliated shoots observed for the branch were plotted against gen_{red}. Similarly, values ranging from 1 to 100, indexed by 10, of $\text{rand}_{\text{main}}$ (the year at which the main axis became subject to the random Poisson process) were investigated.

Results

Model analysis

Sensitivity analysis: **Pseudotsuga menziesii** *rule combinations 1–3*

Allowing SCUs to develop on both epicormic and lateral axes (RC1–3; Table 3) has a profound effect on model output. Even at the default bifurcations the total foliated shoots at Y90 is impossibly high, causing a memory error on the computer. This rule for SCU independence places the cumulative effects of reiteration on all lateral shoots, effectively increasing the bifurcation of shoots of ever increasing order. This allows sequential reiteration to occur on lateral axes throughout the branch. Given the simulations, this level of sequential reiteration in combination with proleptic reiteration cannot occur in *P. menziesii*.

Pseudotsuga menziesii *rule combination 4*

Rule combination 4 (RC4; Table 3) requires SCUs to develop only on epicormic axes, and epicormic initiation is not subject to any restrictions beyond the age at sprout determined by the gamma distribution. Under these rules the maximum of total shoots at Y90 with increasing bifurcation is greater than for RC5 and RC6 across all orders and is again largest with increasing order 3 bifurcation and the average bifurcation of newly· initiated epicormic shoots (Fig. 6). Under RC4 there are no restrictions on epicormic initiation, hence the process of reiteration is enhanced; the effects of increases in the parameter values are amplified, because they are in effect in greater numbers of SCUs across the branch.

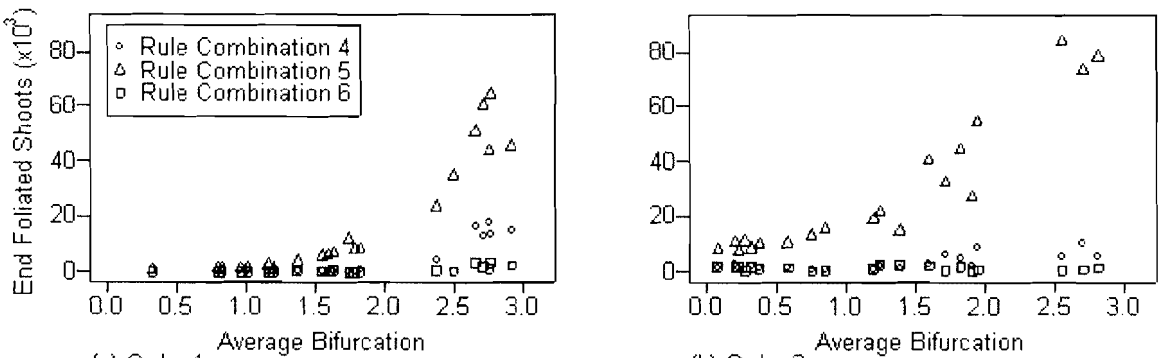
Under RC4, there is an increase in total SCUs with both order 1 and initiated epicormic bifurcations, but no relationship with the bifurcations of orders 2 and 3 (Fig. 7). The magnitude of the effects of increasing order 1 and new epicormic average bifurcation is greater than for RC5. Across all bifurcations the number of SCUs is greater than the number of SCUs formed under RC5 and RC6.

Pseudotsuga menziesii *rule combination 5*

Under Rule combination 5 (RC5; Table 3), SCUs are assumed to develop solely on epicormic shoots, not on lateral axes, and epicormic initiation is limited by the requirement of one inactive lateral axis. In general, total foliated shoots show a nonlinear increase with increasing parameter values (Fig. 6). The maximum total foliated shoots at Y90 is greatest for increases in order 3 bifurcation and the bifurcation of newly initiated epicormic shoots, whereas the maximum for increases in bifurcations of orders 1 and 2 are much smaller (Fig. 6). It should be noted that to save computation time if the simulated branch developed more than 200,000 foliated shoots, the simulation was terminated, and that total was recorded as the end number of foliated shoots. Any point in Fig. 6 that is above 200 000 foliated shoots actually represents the foliated shoots the year the simulation terminated, not necessarily Y90.

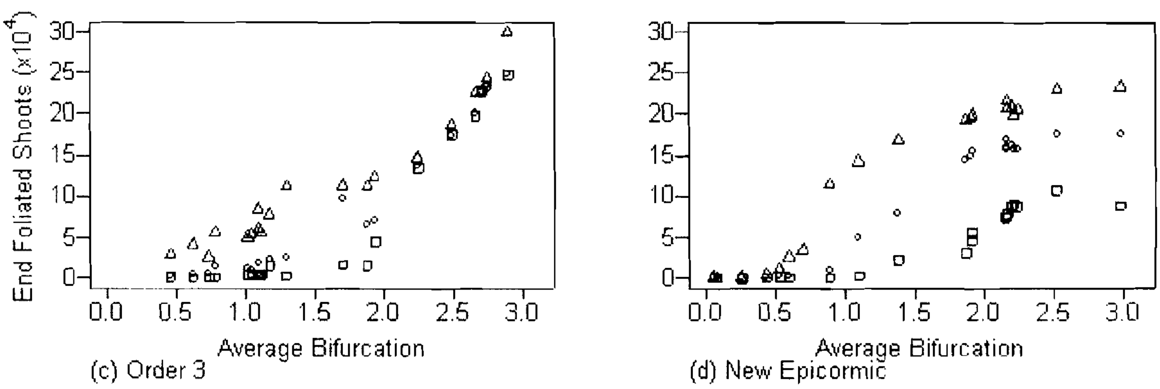
Slightly different results are obtained with total SCUs at Y90. There is some increase with increasing order 1 average bifurcation (Fig. 7), but there is a slightly negative relationship between total SCUs and increases in order 2 bifurcation (Fig. 7). There appears to be little to no trend with increases in order 3 average bifurcation, although for higher bifurca-

Fig. 6. Foliated shoots at year 90 of *Pseudotsuga menziesii* with increasing average bifurcation of (*a*) first-, (*b*) second-, and (*c*) third-order shoots, and (*d*) new epicormic shoots at three different rule combinations. Note the different scale for foliated shoots of third-order and new epicormic shoots. In general foliated shoots increase nonlinearly with increasing average bifurcation of differently ordered shoots. The magnitude of the effect increases when there are fewer restrictions on reiteration and is highest for third-order bifurcation, increasing in the average bifurcation of newly initiated epicormic shoots.



(a) Order 1

(b) Order 2



(c) Order 3

(d) New Epicormic

tions the trend is difficult to analyze because of the early termination of the simulation if the branch grows too large. Within the rules of the model, however, order 3 bifurcation is not expected to influence the process of SCU formation. Total SCUs have a high sensitivity to increases in the average bifurcation of newly initiated epicormic shoots, yielding by far the largest number of total SCUs (Fig. 7).

Pseudotsuga menziesii *rule combination 6*

In rule combination 6 (RC6; Table 3) epicormic initiation is restricted by the requirement of two inactive lateral axes, and SCUs only form on epicormic axes. The maximum simulated total foliated shoots with increasing bifurcation is less than the maximum observed under RC4 and RC5, with the exception of order 3 average bifurcation (Fig. 6). There is no apparent relationship between increasing order 2 bifurcation and total foliated shoots under RC6, because it is difficult for both lateral axes to no longer be growing (a requirement for epicormic initiation) with higher order 2 bifurcation.

The relationship of total SCUs with increasing bifurcation shows a modest increase with increasing order 1 bifurcation, but a steady decline with increasing order 2 bifurcation (Fig. 7). This reflects the further restriction on epicormic initiation set by RC6. The largest increase in total SCUs is seen with higher average bifurcation of new epicormic shoots.

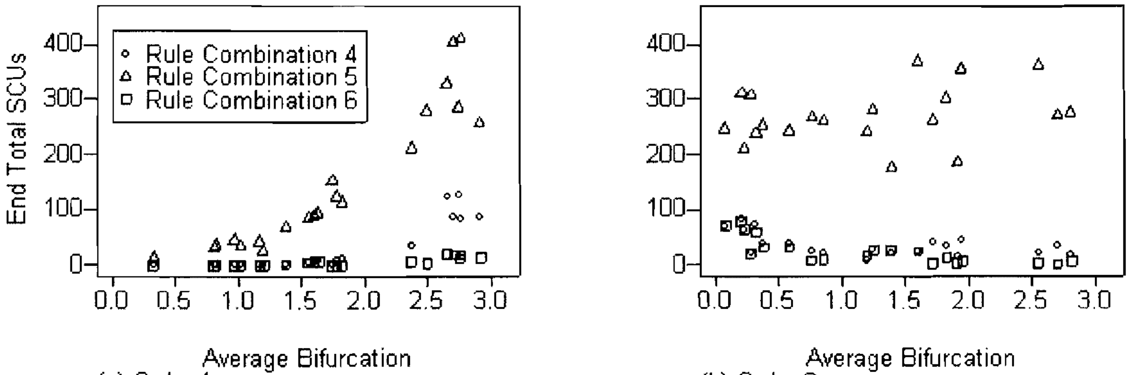
Abies grandis *rule combination 1*

Under rule combination 1 (RC1), SCUs are allowed to develop on both lateral and epicormic axes and the functional role of the SCU becomes possible in *A. grandis* (Table 3). Impossibly high shoot totals were produced under this rule combination, again because of the effects of increasing bifurcation with higher orders of shoots. As with *P. menziesii*, it is obvious that extensive sequential reiteration on lateral shoots is not possible in *A. grandis*. Although *A. grandis* lateral axes have relatively high bifurcations, they are clearly not independent structures that repeat the function of the main axis. Rather, they are morphologically distinct structures within the usual expression of the architectural model.

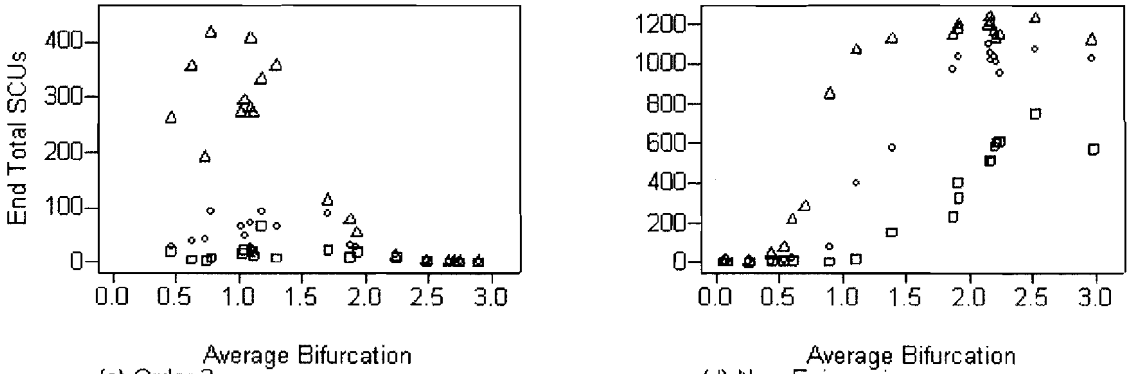
Abies grandis *rule combination 4*

The maximum of total shoots at Y90 was greatest for increases in order 3 bifurcation compared with orders 1 and 2 (Fig. 8; RC4, Table 3). For *A. grandis* the reliance on regular shoot growth results in an increasing effect of higher bifurcation with increasing shoot order. The increase of the average bifurcation of higher ordered shoots is essentially the equivalent of sequential reiteration (dedifferentiation of a lateral axis to reiterate the main axis within the usual timing of growth), which, as mentioned, was seen to have a profound cumulative effect on *A. grandis* branch growth. At the

Fig. 7. Total shoot cluster units (SCUs) for *Pseudotsuga menziesii* at year 90 with increasing average bifurcation of (*a*) first-, (*b*) second-, and (*c*) third-order shoots, and (*d*) the average bifurcation of new epicormic shoots at three different rule combinations. Note the different scale for total SCUs of new epicormic shoots. There is a nonlinear increase in total SCUs with increasing first-order average bifurcation, but no relationship with second-order average bifurcation. The relationship is ambiguous with third-order bifurcation, and there is an increase and leveling with higher average bifurcation of new epicormic shoots. The relationships differ among the rule combinations, with the greatest increases when there are the fewest restrictions on epicormic initiation.

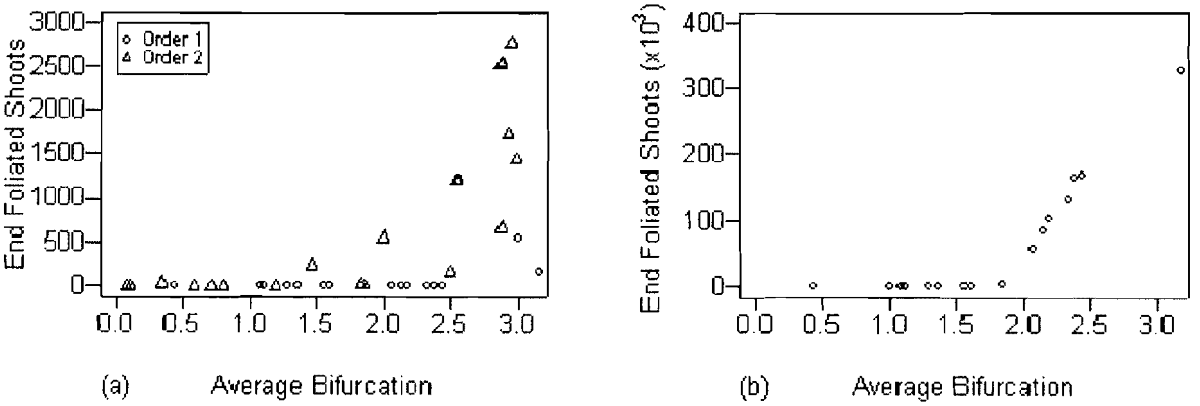


(a) Order 1 (b) Order 2



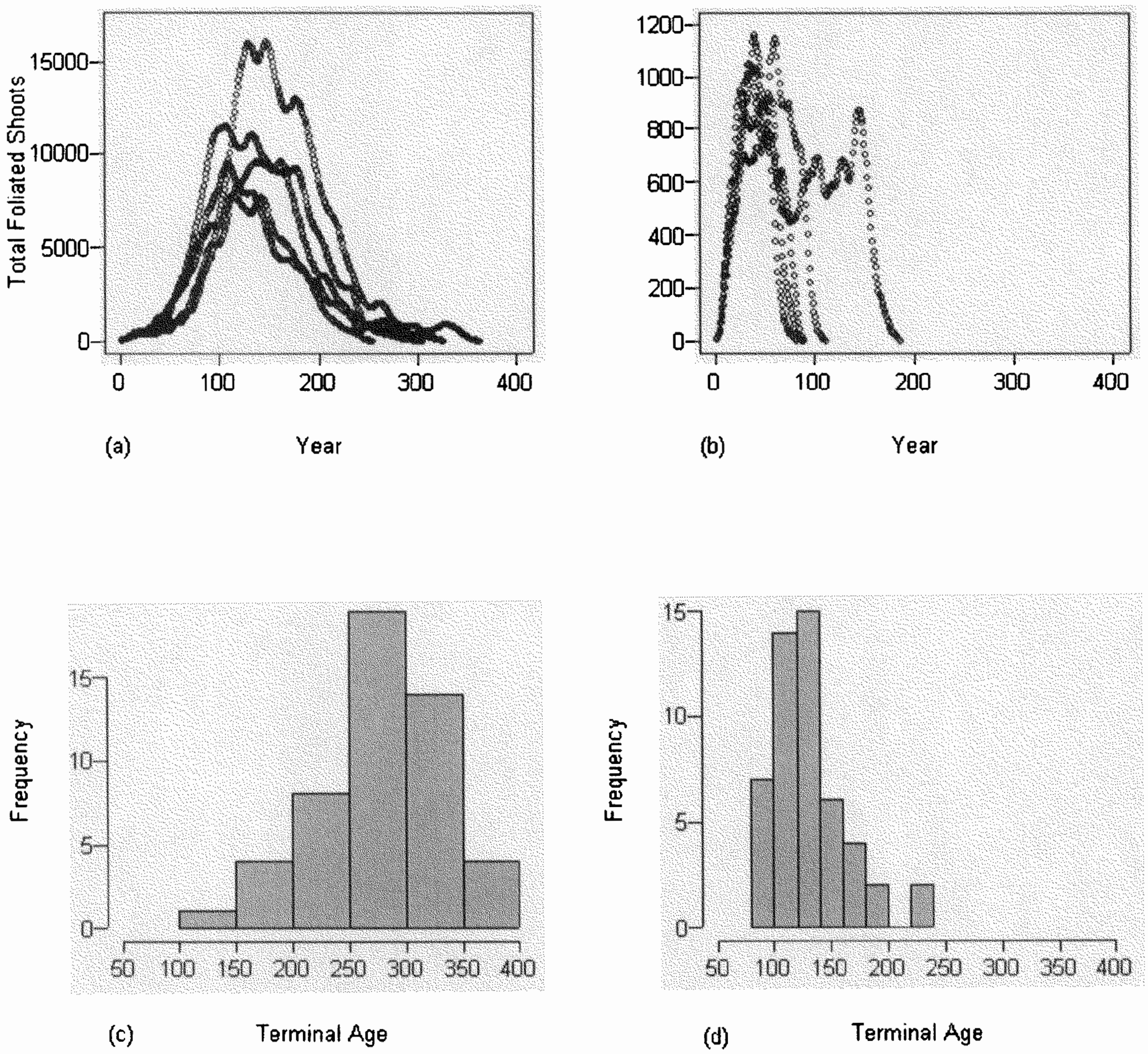
(c) Order 3 (d) New Epicormic

Fig. 8. Total foliated shoots at year 90 in *A. grandis* with increasing bifurcations under rule combination 1. (*a*) Bifurcations of first- and second-order shoots. (*b*) Third-order bifurcation. Increases in all three parameters result in nonlinear increases in total shoots, with the greatest increase shown for third-order average bifurcation.



© 2004 NRC Canada

Fig. 9. (*a*) Total foliated shoots over branch life-span for five simulations of *Pseudotsuga menziesii* at default parameter values (Table 1). (*b*) Frequency histogram of the terminal age of a population of 50 branches of *P. menziesii*. (*c*) Total foliated shoots over branch life-span for five simulations of *Abies grandis* at default parameter values (Table 1). Both species demonstrate fluctuations of foliated shoots over time for all simulations, and *P. menziesii* shows both higher peak total foliated shoots and greater branch longevity. (*d*) Frequency histogram of the terminal age of a population of 50 branches of *A. grandis*. *Pseudotsuga menziesii* has a higher average terminal age than *A. grandis*.



same time, the small effect of increasing order 1 bifurcation is due to the bound imposed on growth: the Poisson process is not used for first-order shoots until Y50, at which time order 1 bifurcation plays a role in the simulation.

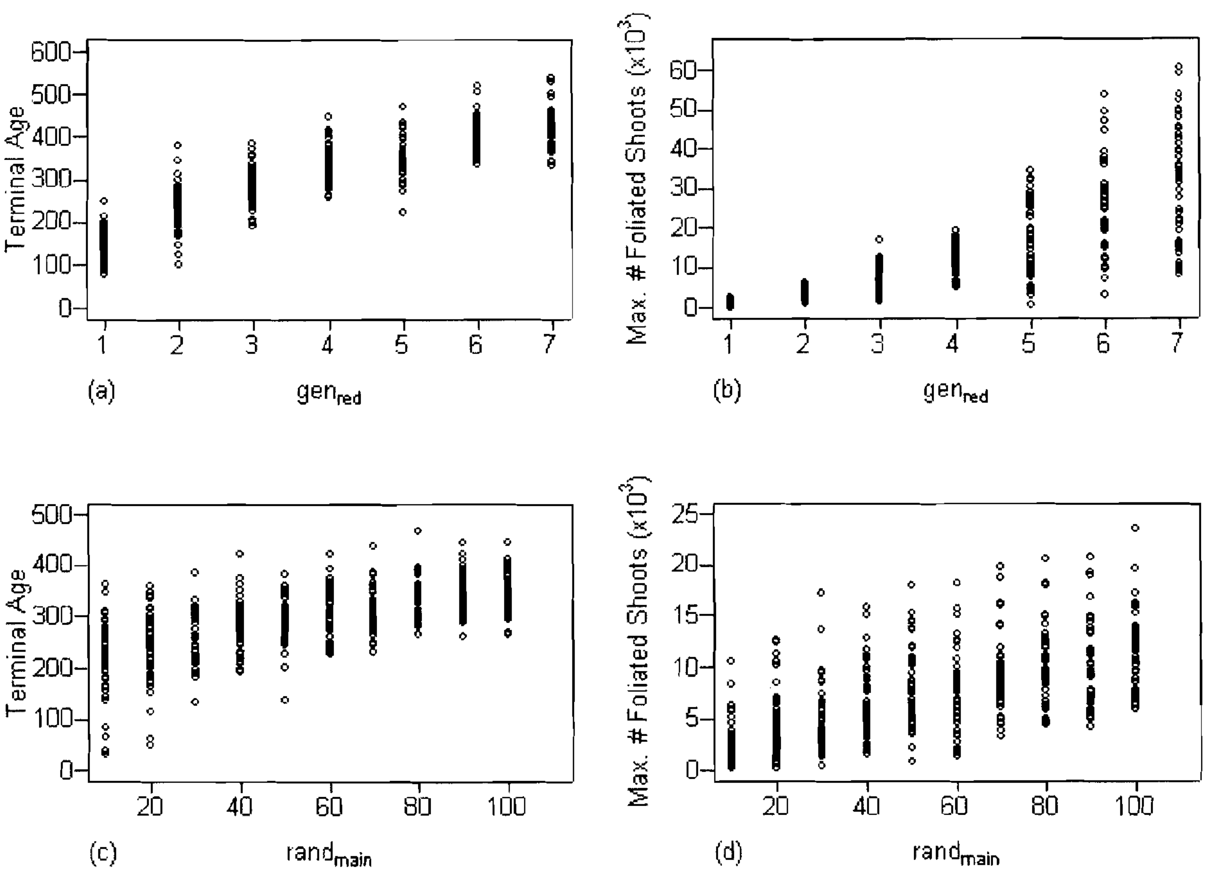
Analysis of potential branch longevity: Pseudotsuga menziesii

Plots of simulated total foliated shoots over time for five different seed values in *P. menziesii* show fluctuating trends of growth, decline, and renewal (Fig. 9). For a population of 50 simulated *P. menziesii* branches the mean terminal age is 281, and all branches terminated before year 400 (Fig. 9). This indicates that the limitation imposed on SCU growth in the simulation model with increasing generation is sufficient to result in the observed decline of the entire branch without the inclusion of factors that are external to the branch (e.g., damage or disturbance). It is likely the death of the branch would occur before the total foliated shoots reaches zero, but this analysis demonstrates that such a mortal decline would eventually occur some time before year 300.

There is a positive relationship between both the maximum number of foliated shoots and the terminal age of simulated branches with $\mathrm{gen}_{\mathrm{red}}$ (the epicormic generation at which initial epicormic growth is reduced, Fig. 10). The variability of the maximum number of simulated foliated shoots also increased with increasing $\mathrm{gen}_{\mathrm{red}}$, which reflects previous observations that enhanced epicormic growth can result in highly variable cumulative effects. There is also a positive relationship between the maximum number of foliated shoots and the terminal age of a simulated branch with

© 2004 NRC Canada

Fig. 10. Plots of terminal age and maximum number of foliated shoots of simulated *Pseudotsuga menziesii* branches. The terminal age of the branch increases with both (*a*) higher gen_{red} and (*b*) higher $\text{rand}_{\text{main}}$. (*c*) The maximum number of foliated shoots on a branch increases with increasing gen_{red} and with increasing (*d*) $\text{rand}_{\text{main}}$. Epicormic growth strongly influences branch longevity and has increasingly cumulative effects on the population of foliated shoots.



increasing $\text{rand}_{\text{main}}$ (the age at which the main axis of a simulated branch became subject to the random Poisson process, Fig. 10).

Analysis of potential branch longevity: Abies grandis

There are some fluctuations in the trend of simulated total shoots over time in *A. grandis* that are not as common or as pronounced as the cycles observed in *P. menziesii* (Fig. 9). This is likely due to the lack of proleptic reiteration in *A. grandis*, which experiences more regular, consistent growth. The fluctuations observed in *P. menziesii* are due to flushes of reiteration over time. The mean terminal age for 50 simulated branches of *A. grandis* is 131.36, much less than observed for simulated *P. menziesii* branches.

SCU development in Pseudotsuga menziesii

The shape of the plot of the total number of SCUs over time for a single simulated branch of *P. menziesii* is similar to that observed for total foliated shoots over time (Fig. 11), with a peak of 90 SCUs around year 135. In branches aged between 126 and 162 years, Ishii and Ford (2001) observed between 86 and 115 total SCUs; the simulated number falls in this range. Both simulated sequential shoots per SCU and new epicormic shoots forming on the SCU show initial fluctuating patterns over time, then steady relationships (Fig. 11). This indicates that in the simulations the average dynamics of SCU growth over time are stable throughout most of the life-span of the branch; it is changes in the population of SCUs that most likely account for variable growth in total shoots on the branch over time. Demographic plots of total epicormic and regular shoots for a given shoot age generated every 5 years for a single simulated SCU (Fig. 12) follow the distributions described by Ishii and Ford (2001, their Fig. 5) in the classification of the stages of SCU development. The simulated SCU explored was declared independent in year 35 (at age 10) and survived through year 60, giving it a life-span of 35 years.

The potential life-span of the SCU can be assessed in the context of the Poisson distribution for the number of daughter shoots per active node. The decrease in expected value for the modified Poisson distribution used in the simulations does not affect the probability of a particular node drawing a zero (i.e., the stochastic death of the terminal bud). If one can assume that the number of daughter shoots produced by the main axis is independent for each consecutive year, then the age at which the main axis of an SCU is expected to draw its first zero can be modeled by a geometric distribution (i.e., the number of "trials" to the first event). If we define the random variable X as the number of years until the main axis draws a zero and assume the probability of

Fig. 11. (*a*) The plot of total shoot cluster units (SCUs) over time for a single simulated branch of *Pseudotsuga menziesii* has a shape similar to total foliated shoots (Fig. 9*a*). (*b*) Average SCU dynamics (foliated regular and epicormic shoots per SCU) are stable over time despite the peak and decline observed in (*a*) for total SCUs.

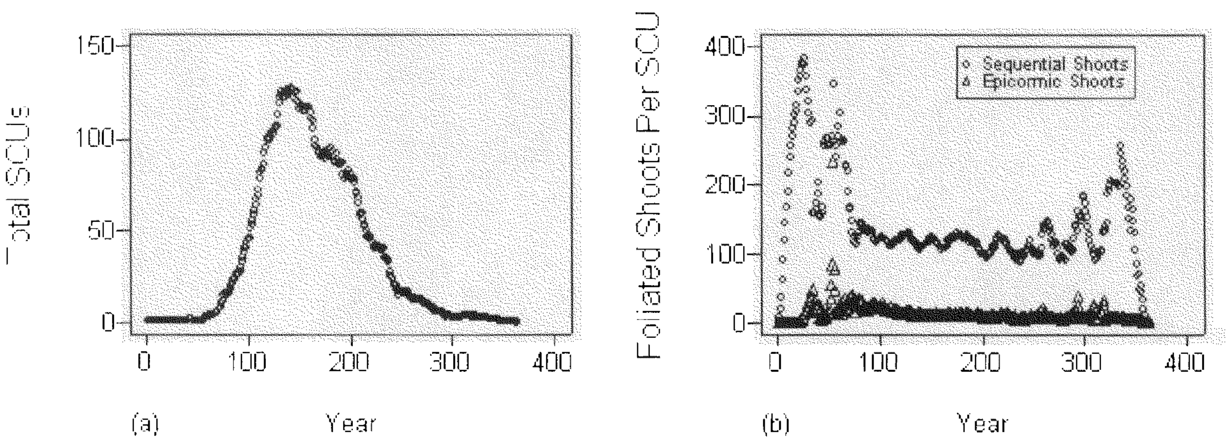
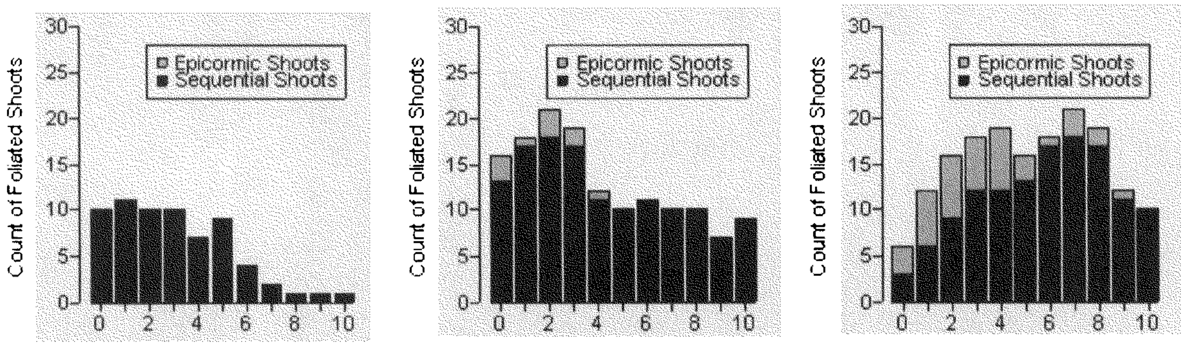
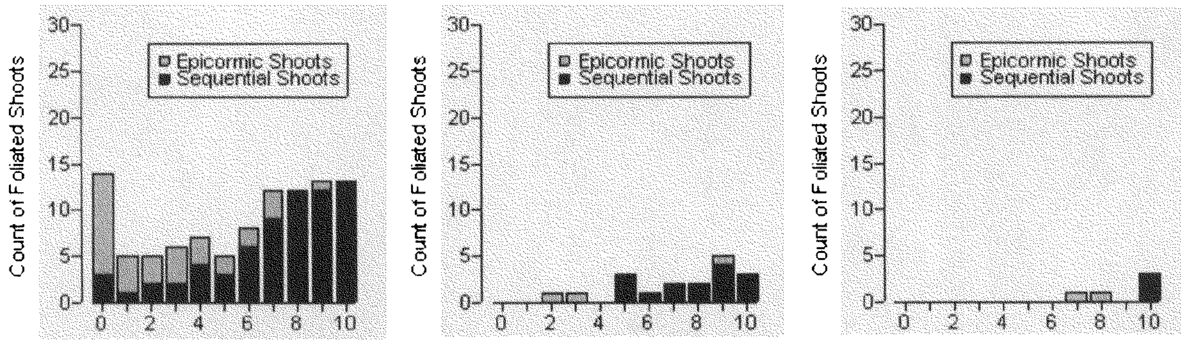


Fig. 12. Plots of shoot cluster unit (SCU) shoot demography for an SCU through years 35–60. The plots were generated every 5 years. The plots exhibit some of the stages of SCU development outlined by Ishii and Ford (2001). (*a*) Initially, there is only sequential growth, with high frequency of younger tissue. (*b*–*d*) As the distribution shifts to older shoots, epicormic growth occurs, regenerating younger age-classes. (*e*–*f*) Eventually, the sequential growth declines and the epicormic shoots have either declined or have formed new SCUs independent of the parent SCU.



(a) Year 35 (b) Year 40 (c) Year 45



(d) Year 50 (e) Year 55 (f) Year 60

drawing a zero is determined by the Poisson distribution, then the probability that the main axis is lost on year X and its expected value are as follows (Casella and Berger 1990):

$$[5]\quad \begin{aligned} &P(k=0)=\frac{\mathrm{Rb}^0 e^{-\mathrm{Rb}}}{0!}=e^{-\mathrm{Rb}} \\ &P(X=x)=p(1-p)^{x-1};\quad x=1,2,\ldots;\quad p=e^{-\mathrm{Rb}} \\ &E(X)=\frac{1}{p}=e^{-\mathrm{Rb}} \end{aligned}$$

For example, if order 1 average bifurcation is 2.5, then it would be expected that the developing order 1 axis would randomly draw a zero at year 12.18. For an order 1 average bifurcation of 3.0 the expected year would be 20.09. Once the main axis is lost the SCU structure quickly deteriorates, with regeneration from epicormics resulting in new SCUs (Fig. 12). The oldest SCU Ishii and Ford (2001) observed was 24, while the average ages of observed SCUs was 11.27, 12.43, and 11.17 for the upper, middle, and lower crowns. If an SCU is expected to lose its main axis at year 12.18, then it would still have foliage-bearing shoots up to 22 years (with 10–11 years being the maximum foliage longevity). It seems that this probability structure adequately matches the observations of SCU longevity.

Discussion

Question 1: How does epicormic sprouting result in SCUs?

Cline (1997) describes four stages of apical dominance: lateral bud formation, imposition of inhibition of lateral bud growth, release of apical dominance, and branch shoot development. These stages reflect what occurs in the initiation of epicormic shoots as described previously. In addition to hormonal control (e.g., Cline 1991, 1994; Bollmark et al. 1995; Hao-Jie et al. 1996; Cline 1997; Miguel et al. 1998; DeWit et al. 2002), both nutrients and light have been implicated in the release of apical dominance (Martin 1987; Cline 1991). It is possible that both the loss of the subtended lateral apex (see rules 2 and 3 for epicormic initiation) and the corresponding favorable light and nutrient conditions for growth along the main axis are necessary for the release of suppressed epicormic buds. This would enable the branch to continue exploiting areas conducive to growth along its axis where the limits of foliage mortality have left a non-photosynthetic twig bare. *Pseudotsuga menziesii* has a lower branch density than *A. grandis* (number of branches per metre of stem; data for *P. menziesii* can be found in Ishii and Wilson (2001); for *A. grandis*, H. Ishii and D.C. Shaw, unpublished data), and it has been observed that *A. grandis* has a higher average bifurcation than does *P. menziesii* on lateral axes (Ishii et al. 2003). We suggest that the more diffuse crown of *P. menziesii* provides greater light transmission through to the lower crown and the inner core of the crown than *A. grandis*, which provides the microenvironment necessary for reiteration to occur. When the suppressed bud is released, it grows as if surrounding tissue does not influence it, that is, it acts as an independent main-branch axis.

The rules for SCU independence used in the model reflect two layers of what is meant by an independent cluster of foliage. Throughout this analysis independence is defined by apical dominance. In a limited sense and under certain circumstances, branches can be assumed to function autonomously with regard to carbon (Sprugel et al. 1991, Sprugel 2002), but we make no such assumptions about SCUs.

In the first rule of independence that was explored, SCUs are identified through morphological distinctness, that is, any axis that is no longer connected to the main axis via live foliage can be considered an SCU. An implicit assumption of this rule is that morphological distinctness is sufficient to cause release of the lateral axis from dominance of its associated main axis (sequential reiteration), allowing for greater bifurcation of the lateral axis (rule 1 for SCU independence). If such morphologically distinct lateral axes throughout the branch are then given order 1 (i.e., reiterated to be like the main axis), simulated growth explodes to impossibly high numbers of foliated shoots. In *A. grandis*, higher average lateral bifurcation results in lateral axes that visually resemble SCUs, but these should not be considered reiterations of the main axis. In the definition of the first rule for SCU independence the morphological characteristics precede the associated physiological function of the growing axis.

In the second rule for SCU independence the physiological function precedes the architectural characteristics; it is only on epicormics that have been observed to function as first-order shoots that SCUs are allowed to develop (i.e., the main-axis function precedes the classification into SCUs). In *P. menziesii*, SCUs that developed from epicormic sprouting resulted in simulated branches that were reasonable relative to the observed branches (Fig. 4*f*, Table 4). The key to this distinction between *A. grandis* and *P. menziesii* is the recognition of the developmental origin of the shoot grouping. It is also possible for a sequential lateral axis to function as a first-order axis, such as after a trauma to the main terminal bud; in this case the sequential axis may produce an SCU. The issue is how to determine whether the new axis is physiologically independent from the first-order main axis.

The trends of total foliated shoots and SCUs with increasing average bifurcation seen in the sensitivity analysis can be explained by the relationship between the rules for epicormic initiation and SCU independence. Under all rules, there is a minimum number of shoots that an epicormic complex must have to be called a new SCU (10 shoots), and epicormics can only form on order 1 axes. Therefore, increases in order 1 bifurcation facilitate the process of SCU formation by increasing the number of order 1 nodes available for epicormic initiation (Figs. 6*a*, 7*a*). Higher order 1 and 2 bifurcations also increase the likelihood that a newly forming SCU produces sufficient shoots to reach the minimum number necessary for SCU independence (Figs. 6, 7). However, if epicormic initiation requires one or both of the subtended lateral axes to be terminated (RC5, RC6), then higher order 2 bifurcation would decrease the probability that an epicormic initiates. Due to these competing forces under RC5 there is a slightly negative relationship between order 2 bifurcation and the total number of SCUs on the branch (Fig. 7*b*). This is further amplified if both subtended shoots must no longer be growing, as in RC6.

With respect to question 1, we conclude that epicormic sprouting results in SCUs through a combination of physiological controls and plant architecture. Epicormic sprouting allows the basic architectural model of *P. menziesii* to be reiterated relatively independently along the horizontal main-branch axis, even after the branch has reached its maximum length (i.e., crown expansion has ceased).

The reiteration of SCUs defined for *P. menziesii* occurs on a smaller scale than the reiteration described by Hallé et al. (1978) in tropical trees. Hallé et al. (1978) observed vertical reiterations of the architectural model of the entire tree, resulting in "mini trees" throughout the crown. Although Hallé et al. (1978) describe a limited number of basic architectural models in tropical trees, they also note great diversity among trees that share an architectural model. Often this diversity is due to the way in which the model is reiterated during crown development. In *T. plicata*, Edelstein and Ford (2002) observed smaller scale vertical reiterations along horizontal-branching axes. In the case of *P. menziesii* the observed reiteration occurs horizontally along the branching axis and repeats the growth of branches, not the vertical growth of the main stem. Through reiteration a tree exhibits opportunistic architecture that allows for diversity in the way the crown exploits available resources.

Question 2: What are the advantages of reiteration?

It is clear that reiteration contributes significantly to the growth of *P. menziesii*, resulting in observed branches up to 155 years old (Ishii and Ford 2001) and simulated branches that contained foliated shoots for up to 393 years (Figs. 9*a*, 9*c*). In contrast, the oldest observed branch of *A. grandis* was only 63 years old, and simulated branches lived up to 226 years, with no contribution of reiteration to growth (Table 4, Figs. 9*b*, 9*d*). Sensitivity analysis shows that small increases in average bifurcation of higher order shoots propagate throughout the branch and result in drastic increases in total foliated shoots (Figs. 4*c* and 8*b*) that are densely located distally on the branch. Furthermore, a small increase in the ability of the branch to reiterate (either proleptically or on sequential axes) also has a profound effect on the total number of foliated shoots on the branch (Figs. 4, 10*a*, 10*b*). Even a restricted capacity for reiteration has a strong cumulative effect on the ability of the branch to survive through regeneration of its foliage (Fig. 4).

It has been observed that growth declines with increasing age and complexity (Moorby and Wareing 1963; Fisher and Honda 1977; Zimmerman 1978; Clark 1983; Borchert and Honda 1984; Bond 2000), with many explanations for how greater complexity can be detrimental. Wilson (2000) claims apical control regulates the amount of elongation and diameter growth in trees and branches, possibly through a reduction in the transport of water and nutrients to lateral shoots. Zimmerman (1978) found a distinct hydraulic constriction at branching junctions, while Borchert and Honda (1984) observed that flux (not defined by authors) decreased with increasing order, and reductions in bifurcation of higher branching orders was due to the exponential decrease in the flux of lateral branches. Hubbard et al. (1999) propose increasing numbers of branch junctions along conductance pathways as one of the possible alternative explanations for differences in hydraulic conductance and leaf gas exchange between tall and short trees. Niinemets (2002) concluded that size has a greater effect on decreasing stomatal conductance than on age in *P. abies* and *Pinus sylvestris*. To effectively simulate branches of *P. menziesii*, we found it necessary to include a parameter that restricted complexity caused by reiteration (gen_{red}) and to reduce bifurcation with increasing generation (Fig. 4, eq. 4). This also effectively reduced the influence of the strong stochastic effects observed in the model, although the simulations still exhibited extensive stochasticity. The limitation, however, was imposed to observe desired ranges of model outputs and do not yet have a basis in field observations.

To answer question 2, we conclude that reiteration of the SCU in *P. menziesii* profoundly increases the life-span of branches relative to *A. grandis*, and reiteration is shown to have a significant cumulative effect on growth. The utilization of existing meristems to regenerate foliage on established branch axes and in the absence of additional branch length is a powerful method of crown maintenance in *P. menziesii*.

It is possible that a limited form of traumatic sequential reiteration should be simulated on these branches as a reasonable alternative to forcing the main axis to persist for the first 50 years of branch growth. With the loss of the terminal bud, sequential lateral shoots would be released from apical dominance and assume the role of the main axis within the usual timing of growth, as has been observed in the vertical growth of branches in various species (e.g., Harding 1986). Traumatic reiteration would be expected to increase the life-span of both species, although limitations on complexity may need to be imposed in this case as well. In addition, some basal reiteration has also been observed in *P. menziesii* (Ishii et al. 2002), where suppressed buds initiate on older branch axes (up to 60 years old, about 23 years on average). The incorporation of epicormic sprouting on older suppressed buds may allow for reiteration to occur without restriction, where lower generations of SCUs are continually forming at all stages of branch development. In this case reiteration provides a potentially limitless source of new foliated tissue (Lanner 2002) on the branch.

The study of the SCU

To aid further investigation we propose the classification of SCUs into their developmental origins: proleptic (via epicormic sprouting) or sequential (on lateral sequential axes in response to the loss of the apical meristem). The properties of these organizational units can be compared to determine whether the SCU is truly a fundamental unit throughout the branching structure of *P. menziesii* or whether its definition is restricted to growth via epicormic sprouting. In addition, the local environmental conditions of the branch in the proximity of newly developed SCUs can be investigated and compared with areas without SCUs to delineate the cause of epicormic sprouting and SCU development. Finally, the growth of newly sprouted epicormics classified by generation can be quantified to determine whether growth declines with increasing generation or if generation influences the success of epicormic sprouting on a *P. menziesii* branch.

Acknowledgements

The data for this research were gathered 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. Financial support was provided through a grant from the Andrew W. Mellon Foundation. The authors wish to thank two anonymous reviewers for their helpful comments, and Douglas Sprugel and Judith Zeh for useful comments and support throughout this research project. We would also like to thank Annette Hamilton, Dave Shaw, and Mark Creighton for their assistance in the study and many student and part-time workers for their assistance in the field and laboratory.

References

Begin, C., and Filion, L. 1999. Black spruce (*Picea mariana*) architecture. Can. J. Bot. **77**: 664–672.

Bollmark, M., Hao-Jie, C., Moritz, T., and Eliasson, L. 1995. Relations between cytokinin level, bud development and apical control in Norway spruce, *Picea abies*. Physiol. Plant. **95**: 563 568.

Bond, B.J. 2000. Age-related changes in photosynthesis of woody plants. Trends Plant Sci. **5**: 349–353.

Borchert, R., and Honda, H. 1984. Control of development in the bifurcating branch system of *Tabebuia rosea*: a computer simulation. Bot. Gaz. **145**: 184–195.

Borchert, R., and Slade, N.A. 1981. Bifurcation ratios and the adaptive geometry of trees. Bot. Gaz. **142**: 394–401.

Bryan, J.A., and Lanner, L.M. 1981. Epicormic branching in Rocky Mountain Douglas-fir. Can. J. For. Res. **11**: 190–199.

Campolongo, et al.F., Saltelli, A., and Tarantola, S. 2000. Hitchhiker's guide to sensitivity analysis. *In* Sensitivity analysis. *Edited by* A. Saltelli, K. Chan, and E.M. Scott. John Wiley and Sons, LTC, New YorkWest Sussex. pp. 15–47.

Casella, G., and Berger, R.L. 1990. Statistical inference. Duxbury Press. Belmont, Calif.

Clark, J.R. 1983. Age-related changes in trees. J. Arboric. **9**: 201–205.

Cline, M.G. 1991. Apical dominance. Bot. Rev. **57**: 318–358.

Cline, M.G. 1994. The role of hormones in apical dominance. New approaches to an old problem in plant development. Physiol. Plant. **90**: 230–237.

Cline, M.G. 1997. Concepts and terminology of apical dominance. Am. J. Bot. **84**: 1064–1069.

Cline, M.G., and Sadeski, K. 2002. Is auxin the repressor signal of branch growth in apical control? Am. J. Bot. **89**: 1764–1771.

DeWit, I., Keulemans, J., and Cook, N.C. 2002. Architectural analysis of 1-year-old apple seedlings according to main shoot growth and sylleptic branching characteristics. Trees (Berl.), **16**: 473–478.

Edelstein, Z.R., and Ford, E.D. 2002. Branch and foliage morphological plasticity in old-growth *Thuja plicata*. Tree Phys. **23**: 649–662.

Fisher, J.B., and Honda, H. 1977. Computer simulation of branching pattern and geometry in *Terminalia* (Combretaceae), a tropical tree. Bot. Gaz. **138**: 377–384.

Ford, E.D. 1985. Branching, crown structure and the control of timber production. *In* Attributes of trees as crop plants. *Edited by* M.G.R. Cannell and J. Jackson. Institute of Terrestrial Ecology, Cambridge. pp. 228–252.

Ford, R., and Ford, E.D. 1990. Structure and basic equations of a simulator for branch growth in the Pinaceae. J. Theor. Biol. **146**: 1–13.

Ford, E.D., Avery, A., and Ford, R. 1990. Simulation of branch growth in the *Pinaceae*: interactions of morphology, phenology, foliage productivity and the requirement for structural support, on the export of carbon. J. Theor. Biol. **146**: 15–36.

Franco, M. 1986. The influence of neighbors on the growth of modular organisms with an example from trees. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. **313**: 209–225.

Hallé, F., Oldeman, R.A.A., and Tomlinson, P.B. 1978. Tropical trees and forests: an architectural analysis. Springer-Verlag, New York.

Hao-Jie, C., Bollmark, M., and Eliasson, L. 1996. Evidence that cytokinin controls bud size and branch form in Norway spruce. Physiol. Plant. **98**: 612–618.

Harding, R.B. 1986. Terminal leader failure in white spruce plantations in northern Minnesota. Can. J. For. Res. **16**: 648–650.

Honda, H. 1971. Description of the forms of trees by parameters of the tree-like body: effects of branching angle and branch length on the shape of the tree-like body. J. Theor. Biol. **31**: 331–338.

Honda, H., and Fisher, J.B. 1978. Tree branch angle: maximizing effective leaf area. Science (Washington, D.C.), **199**: 888–890.

Hubbard, R.M., Bond, B.J., and Ryan, M.G. 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. Tree Physiol. **19**: 165–172.

Ishii, H. 2000. A canopy perspective of community dynamics of an old-growth *Pseudotsuga-Tsuga* forest. Ph.D. thesis, College of Forest Resources, University of Washington, Seattle, Wash.

Ishii, H., and Ford, E.D. 2001. The role of epicormic shoot production in maintaining foliage in old *Pseudotsuga menziesii* (Douglas-fir) trees. Can. J. Bot. **79**: 251–264.

Ishii, H., and Wilson, M.E. 2001. Crown structure of old-growth Douglas-fir in the Western Cascades Range, Washington. Can. J. For. Res. **31**: 1250–1261.

Ishii, H., Ford, E.D., and Dinnie, C.E. 2002. The role of epicormic shoot production in maintaining foliage in old *Pseudotsuga menziesii* (Douglas-fir) trees II. Basal reiteration from older branch axes. Can. J. Bot. **80**: 916–926.

Ishii, H., Ford, E.D., and Sprugel, D.G. 2003. Comparative crown form and branching pattern of four coexisting tree species in an old-growth *Pseudotsuga–Tsuga* forest. Eurasian J. For. Res. **6**: 99–109.

Kennedy, M.C. 2002. A geometric simulation model of foliage regeneration in *Abies grandis* and *Pseudotsuga menziesii*. M.Sc. thesis, Quantitative Ecology and Resource Management, University of Washington, Seattle, Wash.

Kull, O., Broadmeadow, M., Kruijt, B., and Meir, P. 1999. Light distribution and foliage structure in an oak canopy. Trees (Berl.), **14**: 55–64.

Lanner, R.M. 2002. Why do trees live so long? Ageing Res. Rev. **1**: 623–671.

Maillette, L. 1982. Structural dynamics of silver birch II: a matrix model of the bud population. J. Appl. Ecol. **19**: 203–218.

Miguel, L.C., Longnecker, N.E., and Atkins, C.A. 1998. Branch development in *Lupinius angustifolius* L. II. Relationship with endogeneous ABA, IAA and cytokinins in auxillary and main stem buds. J. Exp. Bot. **49**: 555–562.

Martin, G.C. 1987. Apical dominance. Hortscience, **22**: 824–833.

Moorby, J., and Wareing, P.F. 1963. Ageing in woody plants. Ann. Bot. (Lond.), **21**: 291–308.

Niinemets, U. 2002. Stomatal conductance alone does not explain the decline in foliar photosynthetic rates with increasing tree age and size in *Picea abies* and *Pinus sylvestris*. Tree Physiol. **22**: 515–535.

Press, W.H., Teukolsky, S.A., Vetterling, W.T., and Flannery, B.P. 1992. Numerical recipes in C: the art of scientific computing. 2nd ed. Cambridge University Press. New York.

Remphrey, W.R., and Davidson, C.G. 1992. Spatiotemporal distribution of epicormic shoots and their architecture in branches of *Fraxinus pennsylvanica*. Can. J. For. Res. **22**: 336–340.

Sorrenson-Cothern, K.A., Ford, E.D., and Sprugel, D.G. 1993. A model of competition incorporating plasticity through modular foliage and crown development. Ecol. Monogr. **63**: 277–304.

Sprugel, D.G. 2002. When branch autonomy fails: Milton's law for resource availability and allocation. Tree Physiol. **22**: 1119–1124.

Sprugel, D.G., Hinckley, T.M., and Schaap, W. 1991. The theory and practice of branch autonomy. Annu. Rev. Ecol. Syst. **22**: 309–334.

Sutherland, W.J., and Stillman, R.A. 1988. The foraging tactics of plants. Oikos, **52**: 239–244.

Uylings, H.B.M., Smit, G.J., and Veltman, W.A.M. 1975. Ordering methods in quantitative analysis of branching structures of dendritic trees. Adv. Neurol. **12**: 247–254.

Wilson, B.F. 2000. Apical control of branch growth and angle in woody plants. Am. J. Bot. **87**: 601–607.

Zimmerman, M.H. 1978. Hydraulic architecture of some diffuse-porous trees. Can. J. Bot. **56**: 2286–2295.

© 2004 NRC Canada