A Geometric Simulation Model of Foliage Regeneration in *Abies grandis* and *Pseudotsuga menziesii*

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This is to certify that I have examined this copy of a master’s thesis by

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and have found that it is complete and satisfactory in all respects, and that any and all revisions required by the final examining committee have been made.

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Chapter I

Comparative investigation of foliage regeneration in two old-growth species

Introduction

The vegetation of the Pacific coast of North America is dominated by evergreen coniferous forests (Waring and Franklin 1979). The canopy processes of old-growth evergreen coniferous forests are not well understood due to limited access to the canopies of such tall trees (Parker et al. 1992). It is important to understand both the large biodiversity of the canopy and the growth and development of individual trees (Meslow et al. 1983).

In 1994, a construction crane was built in one such old-growth forest, allowing unprecedented access to the crowns of old trees. The Wind River Canopy Crane Research Facility (WRCCRF) is located in the T.T. Munger Research Natural Area (RNA), in the Gifford Pinchot National Forest, southwestern Washington state. This study has utilized the access the crane provides to increase understanding of the architectural structure of the branches and crowns of large, old *Pseudotsuga menziesii* (Douglas fir) and *Abies grandis* (grand fir) trees and how, in a temperate forest, the foliage in a tree that has reached maximum height and crown expansion can be maintained.

Regardless of the enhanced access the crane provides, limitations on study still apply. Destructive sampling in the RNA is limited mostly to the area outside of the reach of the crane, forcing conventional tree access techniques such as rope climbing. Even then the reach of destructive sampling is limited, and strict randomized sampling designs are impossible. As such, results must be taken in the context of the research environment of old-growth coniferous forests.

Reiteration as a concept

Much work has already been done on crown architecture and maintenance in tropical forests. Halle et al. (1978) describe several basic architectural models of tree growth that they claim encompass the gamut of growth forms observed in tropical forests. The architectural model of a tree refers to its usual pattern of growth in a recognizable and characteristic sequence. Halle et al. (1978) also observed that the reiteration of that basic architectural model is a fundamental morphological characteristic of the tree. Reiteration refers to growth that does not constitute the usual expression of the architectural model; rather, with the activation of a meristem, the complete replication of the original architectural model occurs. In the tropics this was observed as tiny trees that extended vertically from lateral branches, repeating the model of growth observed on the main stem of the tree.

There are several classifications of reiteration that are based both on the mechanism that stimulates the reiteration and the way in which the reiteration occurs. Traumatic reiteration is stimulated by some kind of damage to the apical meristem; when the terminal bud is lost, other meristems are activated to act as the apical meristem. Adaptive reiteration occurs in response to a new input of energy to the system; for example, if a gap is created in the forest canopy a tree can respond to the influx of energy with the activation of suppressed or resting meristems. In this case it is not damage to the apical meristem that triggers the reiteration, rather the opportunity to exploit an additional resource. This term is also used more generally to refer to reiteration as a part of the usual growth of a branch, regardless of external stimuli (Ishii and Ford 2001). In a broader sense, reiteration is a way in which a tree can overcome limitations on the growth of existing apical meristems.

Once stimulated, reiteration can occur through two major processes: proleptic and what will hereafter be referred to as sequential reiteration. Sequential reiteration occurs through the change in function of a terminal meristem within the usual sequential pattern of growth. For example, the terminal meristem that is functioning on a second order axis may be dedifferentiated to function like a first order meristem. This term is chosen rather than sylleptic because all growth in *P. menziesii* and *A. grandis* is technically proleptic. Proleptic reiteration occurs on buds that have gone through a period of suppression and are no longer within the usual growth sequence (i.e. are suppressed for greater than one winter season). Proleptic reiteration is triggered by the release of the suppressed bud to form a new complex that reflects the basic architectural model of the species (Figure 1.1).

While the basic architecture of a tree can be described as deterministic, the process of reiteration can be considered an opportunistic process (Halle et al. 1978; Tomlinson 1983). Begin and Filion (1999) found reiteration—both adaptive and traumatic—to be the main characteristic of black spruce (*Picea mariana*) architecture and stated that in the absence of reiteration a tree would rapidly suffer from dieback with the loss of its foliage on the inner part of the crown. These studies show that reiteration on any scale may be an important process in tree growth.

Branch growth in old P. menziesii

Ishii and Ford (2001) found that proleptic reiteration in *P. menziesii* overcomes the limitation of crown expansion in old trees at the WRCCRF. Through a study of the crown form and branching of four species on the site they developed a theory for the coexistence of late-successional species (e.g. *A. grandis*) with the pioneer species *P. menziesii* (Ishii et al. 2000; Ishii 2000). Although *P. menziesii* is considered a pioneer species insofar as it regenerates on bare ground, such as after a stand-clearing fire, it sustains itself in the forest for as much as 700 years and coexists with late-successional species, rather than being replaced by them. In terms of height *P. menziesii* can dominate old forests until the next large disturbance. Ishii and Ford (2001) postulated that *P. menziesii* has an extended lifespan due to its ability to rejuvenate foliage even when the trees had reached their maximum height and crown width. This rejuvenation of foliage is possible due to the ubiquitous epicormic sprouting that Ishii observed in *P. menziesii* branches.

Epicormic shoots sprout from preformed suppressed buds and secondary daughter buds that proliferate from them. These buds are formed in continuity with the apical meristem (Bryan and Lanner 1981), but while regular shoots sprout from buds formed the previous year, epicormics do not grow in the season after bud formation. They remain on their parent shoot for several years while regular growth continues along the branching axis (Ishii and Ford 2001). Some years later the bud can be released from suppression and sprout a new shoot on existing branch structures. This provides new foliage in an area on the branch at which the foliage has aged or fallen off the tree. Ishii and Ford

(2001) suggested that rather than continuing to grow new foliage at the terminal end of the branching axis, *P. menziesii* continuously regenerates foliage using existing branch structures inside the crown of the trees through epicormic shoot growth. Ishii and Ford (2001) found that the epicormics in *P. menziesii* sprouted on average five years after bud formation. Bryan and Lanner (1981) found that the maximum dormancy of epicormic sprouts was 14 years in Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), which is consistent with results reported by Ishii and Ford. Both researchers observed that epicormics form without exogenous stimuli, although Bryan and Lanner observed mainly epicormic branches that formed at the base of first order lateral branches while Ishii and Ford recorded epicormic sprouting throughout the branch structure. Bryan and Lanner concluded that such epicormic branches form a column of foliage around the trunk, and benefit from the increased light transmission down the bole due to the death of lateral branches above them. It may be that rejuvenation of foliage through epicormic sprouting both vertically along the bole and horizontally along the main axis of lateral branches contribute to the longevity of *P. menziesii*. Remphrey and Davidson (1992) also reported the role of epicormic sprouting in crown maintenance of *Fraxinus pennsylvanica*.

The prevalent epicormic sprouting that Ishii and Ford (2001) observed provided the basis for the reiteration of what they termed shoot cluster units (SCU), distinct clusters of foliage on *P. menziesii* branches. The sequential pattern of growth in *P. menziesii* is always proleptic in that the bud undergoes an inactive period before resuming shoot growth. In the current study sequential growth will refer to growth that occurs after only one period of rest, while proleptic reiteration will refer to the initiation of buds suppressed for greater than one period of rest. The basic architectural model of *P. menziesii* consists of a main axis of the branch (the first order directly off the main trunk) that has 2-3 daughter shoots per year with lateral shoots that only have 1-2 daughter shoots per year. In contrast to sequential lateral shoot growth, Ishii and Ford (2001) observed that the proleptic growth of epicormic shoots mimics the main axis of regular shoots with 2-3 lateral shoots per year. They used foliage mortality to distinguish independent SCUs; if a branching structure with a distinct main axis was spatially separated from other such main axes due to death of needles at its base, then it was deemed independent from the rest of the branch. In this manner the whole branch can be divided into independent branching units that are continuously regenerating foliage inside the crown of the tree.

Using the concept of the SCU, Ishii and Ford (2001) observed up to seven generations of foliage on *P. menziesii* branches. A new generation formed from the successful growth of an epicormic shoot. Within this cycle of growth and rejuvenation, Ishii discerned five phases of development of the SCU (Figure 1.2, copied from Ishii). Regular growth is characterized by expanding age classes in an SCU that has not yet begun epicormic growth. From regular growth an SCU can enter decline 1, in which the age class distribution is no longer expanding. Alternatively epicormic initiation can occur when the regular shoots of the SCU are in regular growth, but epicormics are also present. Decline two is characterized by declining age structures when both regular and epicormic shoots are present. Epicormic renewal occurs when the age class distribution exhibits decline in the regular shoots, but expanding age classes of epicormic shoots.

Current Study

While Ishii and Ford (2001) described SCUs as functional architectural units, further observations and a more detailed analysis of Ishii's data suggest that the SCUs he classified into different developmental stages actually represent a continuous spectrum of growth, reiteration and renewal on the branch. While SCUs were established as a convenient sampling unit in the study of large branches, a theory of reiteration through SCU growth was established. I believe further analysis is necessary to delineate and further characterize the concept of the SCU, and whether indeed such functional architectural units exist. A quantification of the rules necessary to model branch growth in *P. menziesii* and observation of that growth over the lifespan of the branch would be key to understanding the role of reiteration in old *P. menziesii* branches, and whether there is a limitation to the renewal of foliage. This can readily be accomplished through the development of an architectural computer simulation model (Chapter II).

Modeling framework

In the development of an architectural computer simulation model (Chapter II) one can observe the actual development and dynamics of the SCU using the rules put forth by Ishii and Ford (2001), and test whether those rules are valid in the context of the lifespan of an entire branch (Chapter IV). It has been demonstrated that basic branching forms can be characterized and produced through the variation of a few simple parameters (Honda 1971) including length, branching angle, and bifurcation ratios. From these parameters more complex relationships between branch form and growth can be studied, including foliage area display and the distribution of foliage along a branching axis (Bell et al. 1979; Honda and Fisher 1979; Tomlinson 1983). Modeling exercises are useful especially in inferring the architectural consequences of particular geometric rules, which in the field would be very difficult (Fisher 1992; Room et al. 1996; Prusiskiewicz 1998). Many of the modeling exercises that have been previously been performed are limited in space and time (usually up through thirty years), and there has not been a computer simulation that incorporated reiteration (Fisher and Honda 1977; Tomlinson 1983). The objective of this study is to integrate a simple geometric simulation model of branch form with morphological parameters measured at the shoot level and the reiteration of branching units in order to better understand branch survival in an old-growth forest.

Bifurcation ratios as indicators of branch growth

The usefulness of the bifurcation ratio as an index of growth in plants and trees has been a subject of debate. Some authors have asserted the bifurcation ratio to be a stable and reliable measure and an appropriate source of comparison of branch vigor and growth (Whitney 1976, Barker et al. 1973). Such comparisons are made with a branch or tree characterized by a single average bifurcation. Other authors suggest that the bifurcation ratio is not an appropriate tool to characterize tree architecture (Borchert and Slade 1981). Borchert and Slade state that bifurcation ratios are not constant both spatially through the structure of a tree (i.e. non-constant across branching order), as well as temporally through the life of a tree. Therefore a branch or tree cannot be represented by a single average bifurcation. Steingraeber and Waller (1986) also found bifurcation ratios to be non-stationary within individual species, trees and branches. While these authors advise against using stationary bifurcation ratios as general and absolute indices of growth within a species, Steingraeber and Waller (1986) say that bifurcation ratios are of use if they are interpreted with regard to patterns of shoot construction and the developmental characteristics of shoot morphology. The inconstancy of the bifurcation ratio over space and time may be true, yet its value as an architectural measure is important to the current simulation model. In the simulations, first, second and third order shoots are given separate values for average bifurcation and those values are allowed to vary independently (Chapter II; Chapter IV). Average bifurcation values are also explored for newly initiated epicormic structures in their first few years of growth.

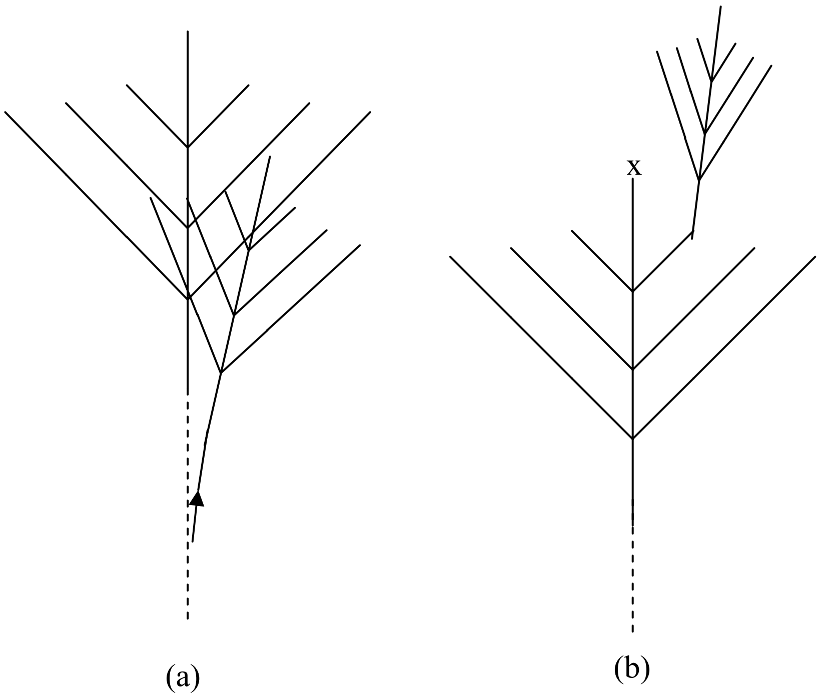
An appropriate contrast

In his book *Ecological Scientific Method*, Ford (2000) describes a framework through which ecologists can make more practical progress in the advancement of ecological theory. Contrary to some of the physical sciences, classical experimental methods are not possible in the study of the complex systems in which ecology is interested. The basis of scientific method, however, is possible on a larger scale in ecology. In simple terms scientists explain the difference between two contrasting situations, usually a control and treatment group. While in ecology rigorous controls and treatments are not often possible, one can still establish an effective contrast (Ford 2000). This is accomplished by choosing two things that are alike in most characteristics, but differ in some important way. The challenge is then to explain how and why they differ.

In order to explain the importance of adaptive proleptic reiteration in *P. menziesii* I chose to study *Abies grandis*, a species also present in the old-growth canopy of the Wind River Canopy Crane facility. Both *A. grandis* and *P. menziesii* exhibit determinate growth, but *A. grandis* does not exhibit the same level of reiteration. Its foliage display is limited to its ability to utilize its active meristems. In a study of branch level foliage characteristics in *A. grandis* and *P. menziesii*, Kershaw and Maguire (1995) presented data for the two species in concert, and the differences between them appeared subtle. In the context of a contrast, these species are much alike, with the exception of the adaptive proleptic reiteration in *P. menziesii*.

Hinckley et al. (1998) suggest that the branch is a useful intermediate unit for scaling from the leaf level to the tree and stand levels, but the starting point for any inferences is measurements made at the leaf level. Ishii and Ford (2001) used measurements of foliage mass, area and shoot demography in their description of branch growth in *P. menziesii*. With these measurements they were able to delineate the foliage support system involved in the functional importance of epicormic sprouting and the reiteration of the SCU. For the purpose of this contrast it is therefore important to observe and describe the foliage support system utilized by branches of *A. grandis* through measurements of shoot demography, foliage area and foliage weight. To further understand the framework upon which each species holds its area and weight of foliage, shoot length, length ratios and branching angles were also measured (Chapter III).

The current study involved three phases. The first phase of the study was the development and writing of the basic structure of the simulation model. A key component to the development and further analysis of the model was the collection of field data for both species, which enabled a more detailed characterization of the individual shoots modeled for the branch. The second step was thus to gather data on the shoot and branch structure of *A. grandis* that could be compared to Ishii and Ford's (2001) data for *P. menziesii,* as well as further analysis of their data. These data served two purposes; the first purpose was to begin the contrast between the two species through a direct analysis of the data. The second purpose was to use the data to help solve the model for parameter values for the two species. Through these two steps the theory of growth Ishii and Ford developed was refined and quantified and an explanation was proposed for how *A. grandis* can coexist with *P. menziesii* in this particular stand. In the final third phase the model was used to discover the characteristics that differentiate the growth of the two species, and it was observed whether a computer simulation can reliably model branch growth over a long period (greater than 100 years). Through the development and analysis of the computer model, differences and similarities between *P. menziesii* and *A. grandis* can then be further defined. Given the importance of reiteration in the maintenance of old branches, a simple question easily follows and was explored: Is there an upper limit to the reiteration observed in *P. menziesii*? That is, without external influence could a branch of *P. menziesii* potentially survive indefinitely through rejuvenation of its foliage with reiteration? A corollary limit to growth in *A. grandis* was also examined.



(a)

(b)

Figure 1.1: A schematic illustrating the distinction between (a) proleptic and (b) sequential reiteration

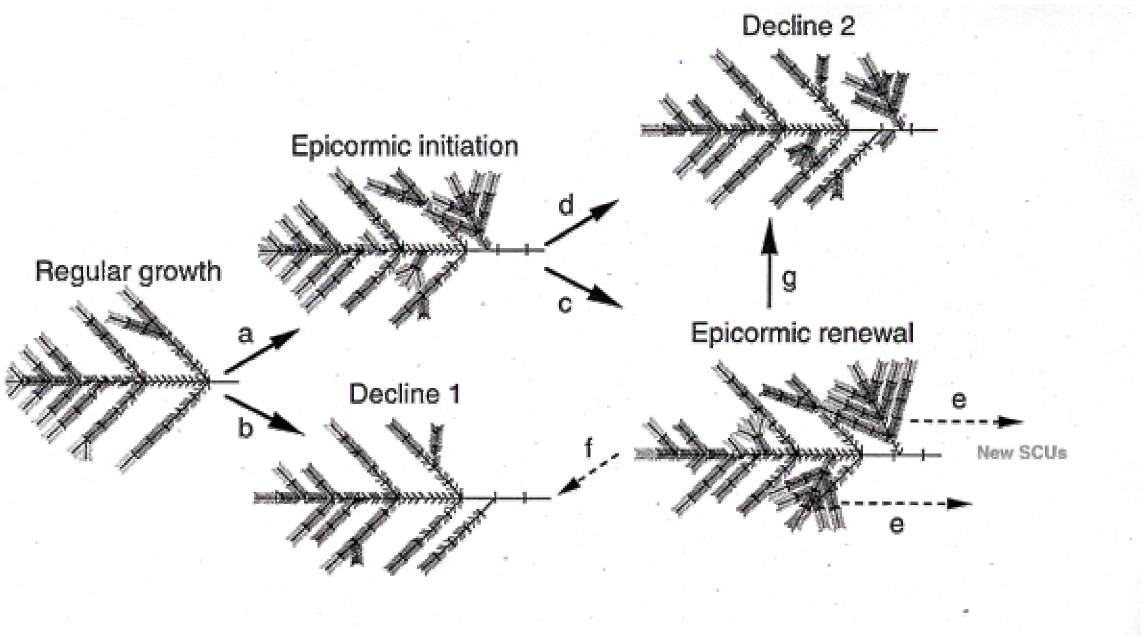


Figure 1.2: Illustration of the stages of SCU development in *P. menziesii* as described by Ishii and Ford (2001), figure from Ishii and Ford.

Chapter II

Development of a basic geometric simulation model of branch growth in *A. grandis* and *P. menziesii*.

Model Background

Reiteration is an important process in the growth of tropical species (Chapter I; Halle et al. 1978), and architectural simulations have demonstrated many important processes of tree growth (Chapter I). Yet, there has not been a simulation model that integrates reiteration into the branching structure of a tree, nor have models been produced which simulated growth over the lifespan of a branch or tree. Early simulation models were based on a few simple parameters for growth up to fifty years, yet many branches studied in the field can survive up through 150 years.

It is important to first understand the difference between the architectural model of a tree as described by Halle et al. (1978) and computer simulation models that are based on tree architecture. Halle et al. (1978) define basic models that describe the usual pattern of growth of a particular tree, such as rhythmic sympodial growth, and use the term architectural model for those patterns of growth. This chapter deals with the creation of a geometric computer simulation model that attempts to take the basic architectural model and translate it into a computer program.

Honda (1971) was the first to observe that the form of trees could be described in simple geometric terms, and that those geometric relationships could easily be translated into a computer simulation. He showed that by using a computer simulation model of tree growth with surprisingly few parameters (initial length, length ratios, bifurcation ratios, branching angles) tree crowns with typical forms could be created. Furthermore, variations in those parameters would result in realistic forms of trees governed by a particular parameter set. From this basic working model, rules and conditions could be added to study the basic ideas necessary to mimic tree forms. This technique has been utilized to study ideas as diverse as the role of branching angle in the maximization of effective leaf area (Honda 1978), the interactions between neighbors of modular organisms (Franco 1986), the effect of different growth parameters on carbon export (Ford et al. 1990), plant competition (Sorrenson-Cothern et al. 1993) and foraging in modular organisms (Sutherland and Stillman 1988). Other modelers have tried to describe branches as populations of buds that have certain probabilities of different fates (Maillette 1982). The current study utilizes the basic geometric modeling technique to study the effect of epicormic shoot formation and the shoot cluster unit (SCU) on the growth of a *P. menziesii* branch. Such a geometric model can also be used to compare the branching strategies of two species that coexist in the same forest stand. As such, a comparison will be made between *P. menziesii* and *A. grandis* trees that exist in the T.T. Munger Research Natural Area, southwestern Washington state.

The model in the current study was written as a geometric model, as described by Sievänen et al. (2000). They distinguish process-based models, geometric models and functional-structural models. In general, process-based models involve the process of tree growth, such as photosynthesis, carbon balance and nutrient balances, while geometric models involve the structural form of a tree, such as architectural parameters used by Honda (1971). Functional-structural models involve both process-based components—photosynthesis—and architectural components (e.g. photosynthesis is related to segment length, or number of shoots in a given area, or coupled with branching angles). For example Ford and Ford (1990) modeled both carbon relations in a branch and the architectural growth of the branch in relation to two conditions (one of which took into account the external environment of the branch). In this context the current study does not involve the process of branch growth. Rather, growth is represented in discrete geometric relationships and there is no provision for including components such as nutrient balance and photosynthesis.

Model development

Shoot order and generation

Shoots are ordered according to the botanical ordering system (Borchert and Slade 1981), which is consistent with the growth of the branch. Shoots that come directly from the trunk are ordered one; lateral shoots are given an order one greater than their parent. A shoot that represents extension of the shoot axis is given the same order as its parent. Since the main objective of ordering segments is to group them with reference to similar functional characteristics (Uylings et al. 1975), this method of shoot ordering was chosen as it represents assumed functional relationships among the shoots in the branching systems. Consistent with the functional theory of reiteration, epicormic shoots are given order one (so that they mimic the properties of the branch main axis) and an independent SCU generated via sequential reiteration is reordered such that the shoots of its main axis are given order 1.

To distinguish the growth of epicormic shoots from regular lateral shoots generations are assigned. All shoots produced through sequential growth are given the same generation as their parent. An increase in bud generation occurs when a suppressed bud is released; the resulting epicormic is given a generation of one greater than its parent. The first shoots grown in the simulation (i.e. those that grow out of the trunk of the tree) are given generation one.

Basic Model

A basic two-dimensional geometric model was designed for *P. menziesii* and *A. grandis*. Table 2.1 shows the basic parameters used in the simple model, and Figure 2.1 is a flow diagram of the model. Much of the language for the basic model was borrowed from the BRANCH model developed by Ford and Ford (1990). Central to the growth of the branch is the bifurcation and extension of individual shoots. A current-year shoot is given four buds, three for potential growth in the next time step and one for suppression and potential epicormic initiation in subsequent time steps. Due to the stochastic nature of branching and the lack of understanding in the causes of the fates of buds (e.g. see Maillette 1982) probability density functions are used to determine which buds grow and which do not.

The simulation model runs on a yearly time step, and growth per year is strictly discrete (Figure 2.1). For each time step the model performs the following functions for each shoot that has been produced to this point:

1) **Regular shoot growth**: if the terminal end of the shoot is active, new shoots are produced at that node. Those buds flagged for growth

(extension or lateral) are grown a particular length, according to order of the shoot and length of its parent (see Chapter III). Each shoot is given a foliage weight and area appropriate to its age and position in the branch (Chapter III), and the new shoots are given four buds, the fates of which are determined by a probability distribution

2) **Epicormic initiation**: Once a shoot is assessed for regular growth, the model tests it for epicormic initiation (see Figure 2.1), that is, whether suppressed buds on the shoot are due to be released from inhibition. Epicormics are assumed to initiate solely on first order shoots on the main axis of SCUs and are assumed to eventually function as first order shoots.

3) **SCU Independence**: The shoot is then tested for whether it satisfies the criterion to become the base of a new SCU. If it doesn't satisfy the criterion then the model moves to the next shoot. If it does, then a new SCU is added to the SCU structure and the shoot and all of the shoots that have grown from it are renumbered as the new SCU.

Model Constants

Table 2.1 gives both the parameters and constants used in the model. Constants are values in the model that are important to growth and have been defined through field studies and data analysis. The main constants are the values for discrete growth and include initial length, subsequent first order growth over time, length ratios between lower and higher order shoots, and lateral as well as epicormic branching angle.

Predictive regression lines were generated for all of these constants (except epicormic branching angle) from a field study of *P. menziesii* and *A. grandis* trees at the WRCCRF during September of 2001 (Chapter III).

Model Parameters

Model parameters are values important for growth that are used in the model but were not determined through observation or could not be extracted from the data (Table 2.1). The effect of the parameters on branch growth can be explored while data driven values are held constant. The main parameters are bifurcation ratios for shoots of different orders. The other two parameters represented 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):

$$P(k) = \frac{\lambda^k e^{-\lambda}}{k!}$$

The Poisson model is utilized in determining growth of a particular shoot. For each newly grown shoot a number k is drawn from a Poisson distribution with a bifurcation ratio as the rate parameter. The algorithm for this random number generation was taken from Press et al. (1992). Subsequently k buds are flagged to grow the following year, with priority 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. The model only supports $k \leq 3$, so any shoots with values drawn greater than three are limited to three daughter shoots, which is the general case observed in the old growth branches studied for both species. This forces a modification of the Poisson distribution, such that the probability of drawing a three is:

$$1\text{-P(0 or 1 or 2)} = 1-\sum_{i=0}^{2}\frac{\lambda^{i}e^{-\lambda}}{i!}$$

and the mean of the distribution is reduced relative to the λ parameter. Any bifurcations explored must thereby be considered in the context of this reduced expected value.

Rules for Epicormic Initiation:

Epicormic initiation (see Figure 1.1) is defined as the release from inhibition of a suppressed bud. Epicormics are assumed to initiate solely on first order shoots and they are eventually given the function of first order shoots. Analysis of Ishii's (2000) data for *P. menziesii* showed a distinct probability distribution for the age of shoots that sprout epicormic branches. A relative frequency distribution was generated of total shoots that sprouted an epicormic at particular ages (Figure 2.2); the probability of epicormic sprouting peaks around five years after the bud is formed, then declines from there. The shape of this distribution resembles the asymmetric gamma 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, i.e. the probability of the time to epicormic initiation is x years. 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. In a generalized and ideal branch (no damage), it is assumed that the gamma density is an appropriate statistical model for age at epicormic sprout in *P. menziesii*. As such, a number is generated from the gamma distribution for each newly grown first order shoot (see Appendix A for a description of random number generation); this number represents the age at which that shoot may sprout an epicormic. For example, if a shoot draws the number five, then the shoot is tested for epicormic initiation during the time step at which that shoot is five years old.

Once a number is drawn and if the shoot satisfies the criterion for epicormic initiation under which the model is running (see below), then an epicormic is produced. If not, the bud is aborted. The 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. Parameters for the gamma distribution were chosen that qualitatively produced a probability distribution that matched the observed values ($\alpha=8$, $\beta=0.7$; Figure 2.2). Although these parameters do not have any biological meaning, they do produce a distribution close to the desired shape. It must be noted here that the age at sprout data were gathered for epicormic shoots that had *already sprouted*. This qualification will need to be addressed in the alternative rules for epicormic initiation.

In the simulation, if a shoot has reached its designated age at sprout then its suppressed bud is tested for epicormic initiation according to three different rules (Table 2.1):

1. **Simple initiation**: under this rule there are no further restrictions on epicormic growth. A shoot deterministically sprouts an epicormic when it reaches its designated age at sprout.
2. **One inactive side**: A possible theory for the release of dormant buds is the requirement that the lateral axis that is subtended from the same node as the suppressed bud is no longer growing. In some respects this is a similar

mechanism to that of release due to damage of the branch, except the cessation of growth occurred for reasons other than external damage. This would explain the ubiquitous observation of epicormics without visible damage to the terminal apex. If the shoot has reached its designated age at sprout and one of its subtended lateral shoots is no longer growing, then the epicormic is sprouted. If both the lateral shoots are still active, the bud is aborted.

3. **Two inactive sides**: in this case both of the lateral subtended shoots must no longer be growing in order for the bud to sprout an epicormic.

The subsequent growth of newly sprouted epicormic shoots for the first few years of growth were determined by a field investigation at the WRCCRF in September 2001 (Chapter III). After two years of growth the epicormic shoots are assumed to function as first order shoots.

Rules for SCU Independence

Each year newly independent SCUs are searched for, and each shoot is assigned an SCU number according to which SCU it belongs. When a group of foliage is defined as a new SCU its main axis is given the same functional role as a first order axis and the shoots are reordered accordingly. This is consistent with the theory of the SCU as a functional reiterative complex. The first challenge is deciding whether one clump of foliage is distinct from another. Two criteria can be discerned from the theory of Ishii and Ford (2001):

1. Contiguity Rule:

The first criterion involves the idea of a cluster of foliage. 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" (quote taken from Ishii, 2000). In this study that criterion is termed the contiguity rule. Under this rule, a lateral axis is assumed independent of the main axis when foliage mortality occurs at the base of the lateral axis, effecting the spatial separation of the lateral axis from the main axis. The original main axis is still considered still part of the parent SCU (maintaining the parent main axis), but the lateral shoots are considered to form the main axis of a new, independent SCU. The shoots of the main axis of this new SCU are then given order one, and the lateral shoots are given orders relative to the main axis. Similarly, when epicormic shoots are spatially separated from the main axis they are also counted as new SCUs. With the contiguity rule, SCUs are formed on both regular and epicormic shoots. This rule provides no functional basis for reiteration other than spatial separation from other foliage-bearing shoots, but it maintains the functional role of reiteration through the reordering of the axis of the independent SCU.

2. Epicormic Rule:

In the second criterion only epicormic shoots form the basis of a new SCU. If the newly forming SCU was older than ten years (the maximum observed foliage longevity) then the SCU was assumed to be an independent unit. This preserves the contiguity criterion for epicormic shoots described above, but lateral shoots are never considered as independent SCUs. This criterion gives a functional basis for reiteration via epicormic shoot growth.

For both rules there is a minimum of ten shoots that can comprise an independent SCU. If the structure has fewer than ten shoots, it is labeled as "miscellaneous"; its shoots are no longer a part of the parent SCU but its growth is insufficient to be an independent SCU. Once an individual SCU is identified under either rule, key characteristics of the SCU in the model are compared to data values gathered for both *P. menziesii* and *A. grandis*. These data comparisons can test which rule for SCU independence is more relevant for either species.

Model output

There are two data structures in the model, one for individual shoots and one for individual SCUs. Data kept in each structure are listed in Table 2.2. These data are sufficient to thoroughly monitor the growth and development of the branch, as well as any subunits of the branch. Each year data of interest can be written to an output file and analyzed as needed. Also recorded are values of total live shoots—epicormic and regular—on the branch, and the sums of foliage weight and area.

Discussion

The adaptation of a basic geometric branch simulation model for particular species is a constructive exercise in and of itself. The quantification of particular rules and parameters defines the scope of knowledge of a particular process. Combined with empirical observation and data, a model can be used to provide structure to a theory and as a laboratory to explore the intricacies of that theory. The process of model development itself is instructive in the context of a given theory.

Through this geometric model branch growth has been broken down into component processes: rules for individual shoot growth and bifurcation with a simple probabilistic structure; values for the foliage weight and area of a given shoot of a given age; and rules for defining reiterative units in the branch structure. While deterministic models have the advantage of consistency and simplicity and have produced realistic images of individual trees, they do not successfully model the range of tree forms within a species found in nature (Fisher and Honda 1977; Bell et al. 1979; Ford 1987). In model analysis, therefore, populations of branches are observed rather than a single representative branch. The ranges of the geometric simulation model in the context of desired model outputs can be explored and compared, as in Sutherland and Stillman (1988). In their analysis of foraging in clonal plants, Sutherland and Stillman (1988) used local changes in branching probabilities, branching angle and internode length to model different foraging tactics, and explored the consequences of changing those parameters on the fraction of ramets in what they termed good sites. Similarly I will explore the effect of changing branching probabilities on the population of shoots of an old branch. This analysis can further the theory of branch growth in *P. menziesii* and *A. grandis*.

Table 2.1:
Parameters and constants used in the simulation model with their abbreviations and values

Constants			
	Description	Possible Values and units	Source
theta	lateral shoot branching angle	+/- $(0,\pi/2)$	Regression (Tables 3.3,3.5)
lrat	length ratio between shoots of different orders	(0,1) unitless	Regression (Tables 3.3,3.5)
sna	Specific Needle Area: the ratio of foliage area to foliage dry weight, used in conjunction with wt.l to predict foliage area of a given shoot.	$(0,\infty)$ cm^2/g	Regression (Tables 3.3,3.5)
wt.l	Weight per length: the foliage dry weight predicted for a given shoot length	$(0,\infty)$ g/cm	Regression (Tables 3.3,3.5)
length	the initial length and subsequent lengths of first order shoots	(0,10) cm	unpublished data (Ishii)
Parameters			
rba	Average bifurcation of first order shoots	(0,4)	none
rbb	Average bifurcation of second order shoots	(0,4)	none
rbc	Average bifurcation of third order shoots	(0,4)	none
epirba	Average bifurcation of newly initiated epicormic shoots	(0,4)	none
rule	Designates which of two rules will be applied for SCU independence	0 or 2	none
eprule	Designates which of three rules will be applied for epicormic initiation	0, 1 or 2	none

Table 2.2:
Values tracked in the data structures of the model. All of data are available for analysis.

Shoot data structure	Data description	SCU data structure	Data description
segment #	identifies the shoot	epi count	the count of live shoots with higher generation than the SCU
parent	identifies the parent shoot of the shoot	shoot count	the count of live shoots the same generation as the SCU
length	length of the shoot	SCU num	identifies the SCU
generation	generation of the shoot	year	the year the SCU is formed (independent of its parent)
theta	branching angle	gen	generation of the SCU
son array	lists the segment numbers of daughter shoots	distance out	position of the SCU
year	year the shoot is formed	age	age of the SCU
foliage	foliage weight on the shoot		
order	shoot order		
active	indicates whether the shoot is available for growth		
SCU num	identifies to which SCU this shoot belongs		
SCU age	age of the SCU to which this shoot belongs		
SCU order	order of the SCU to which this shoot belongs		
coordinates	x and y coordinates that place the shoot on a Cartesian plane for mapping the branch		
mortality	indicates whether the shoot has any live foliage		
age	age of the shoot		
area	foliage area on the shoot		
epi	indicates whether the shoot is epicormic		
distance out	the position of the SCU to which this shoot belongs		
dormant age	the age at which this shoot is expected to sprout		
# sons	the value of the k parameter indicating the number of daughter shoots		

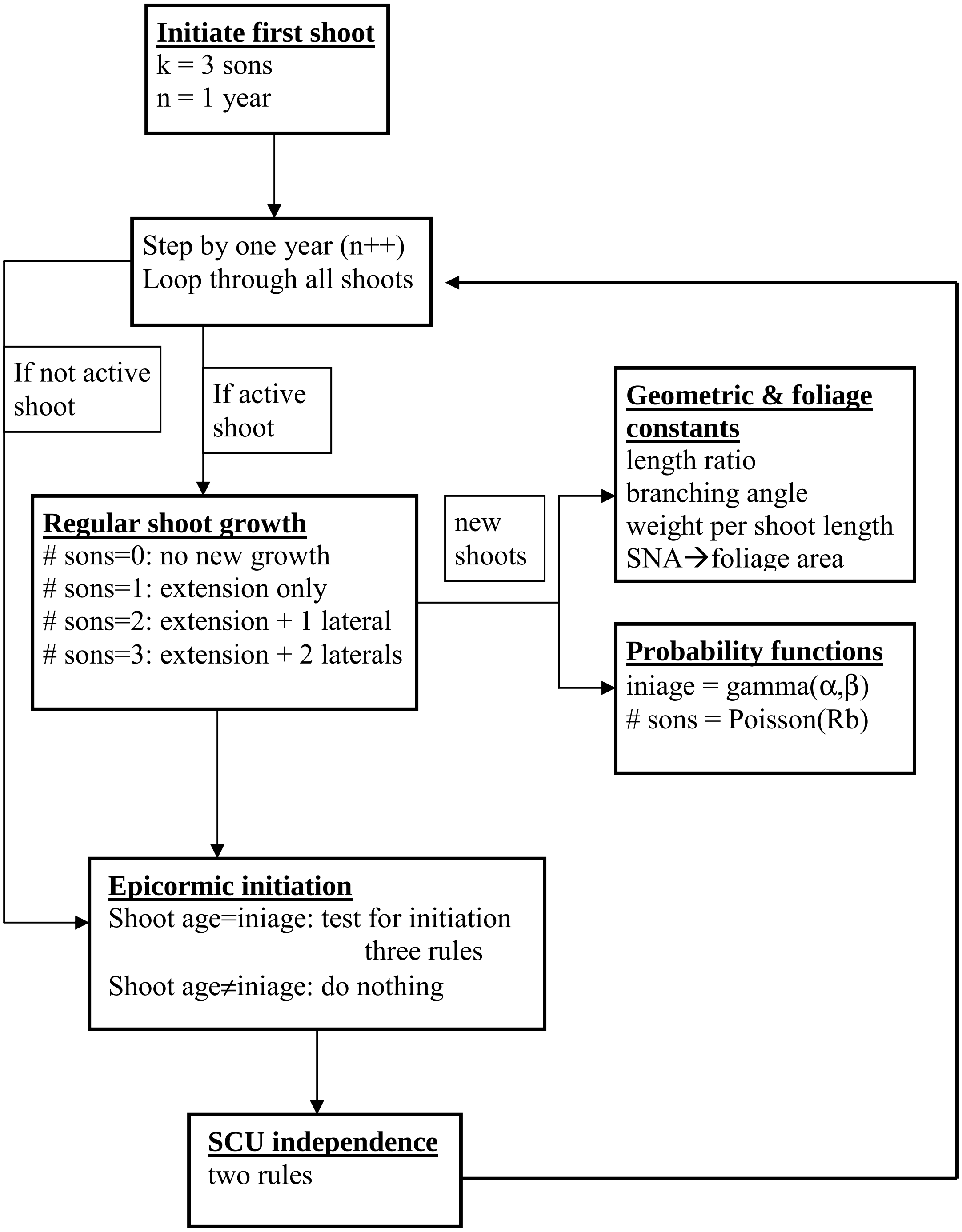


Figure 2.1: Flow diagram for growth in the geometric branch simulation model. After the first shoot is initiated the model begins growth at year two. Every year each shoot in the shoot structure is explored for growth and epicormic initiation and whether it qualifies as the base of a newly independent SCU.

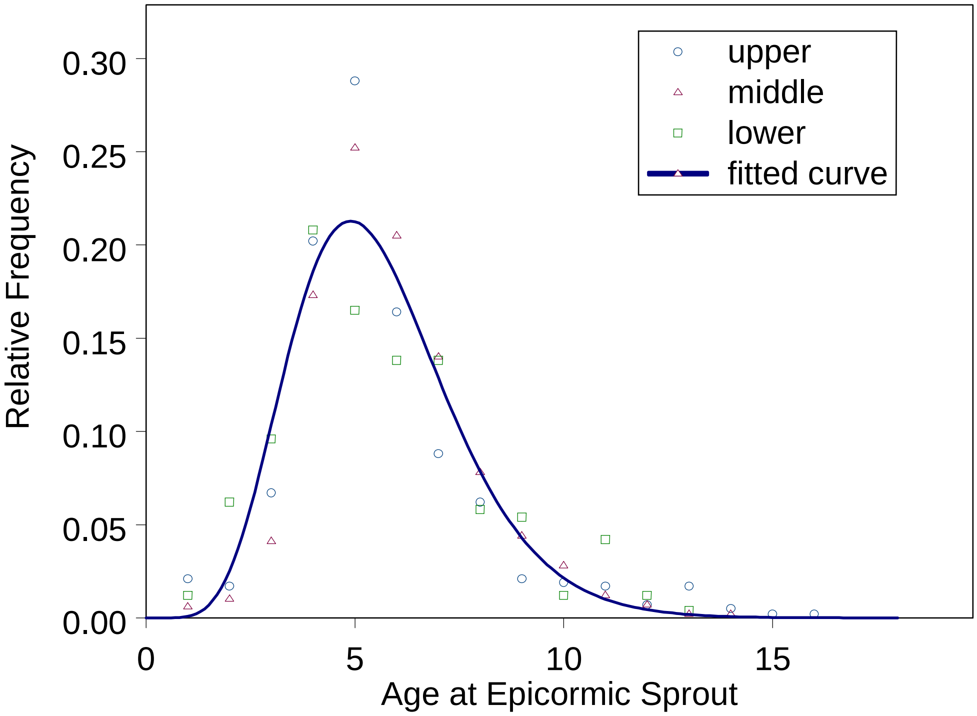


Figure 2.2: Distribution of shoot age at epicormic sprout. The relative frequency distributions show similar shapes at all three crown positions, and a gamma distribution was chosen that approximates the shape of the frequency distribution.

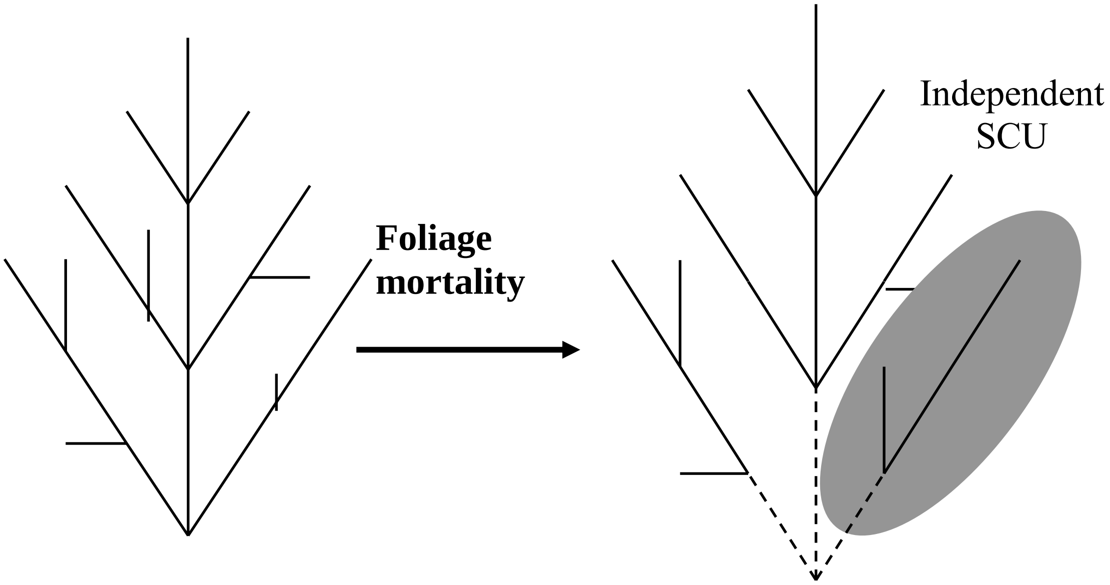


Figure 2.3: A diagram illustrating the process of SCU independence. In this case the process is driven solely by foliage mortality.

Chapter III
Field study of the branching form of *A. grandis* compared to *P. menziesii*.

Introduction

Branch growth in P. menziesii

Ishii and Ford (2001) proposed that architectural acclimation in old *P. menziesii* trees is one way that *P. menziesii* survives and dominates in forests such as those found at the WRCCRF. Acclimation from early-successional conditions to late successional ones includes sparsely branched crowns and a symmetrical pattern of lateral shoot growth. Ishii and Ford (2001) stated that foliage regeneration in old *P. menziesii* occurs through epicormic shoot production, which forms the basis for adaptive reiteration of the shoot cluster unit (SCU). Epicormics allow photosynthetically active foliage to be displayed on already existent branch structure. Such regeneration was not observed on other trees on the same site, yet several species have been predicted to reach ages and heights similar to those *P. menziesii* has achieved (Ishii et al. 2000). In the analysis described by Ishii et al. (2000) and Thomas (1996) a maximum height estimate was calculated for *A. grandis* on the Wind River site. Ishii et al. report the predicted maximum height of *P. menziesii* was 60.1 m. In a similar analysis presented here for *A. grandis* the maximum height was estimated to be 51.0 meters (see Appendix B), with some trees exceeding that predicted height (53.2 m). Although *A. grandis* probably will never grow as large as *P. menziesii*, there are several trees that have attained the maximum height for the species (data provided by the Wind River Canopy Crane Research Facility). This indicates that *P. menziesii* will continue to dominate *A. grandis* in terms of height in this stand.

Ishii demonstrated the process of foliage renewal in *P. menziesii* through a dissection of branches of old *P. menziesii* trees. He analyzed demographic data on the SCU and foliage area and mass measurements on individual shoots. All measurements were repeated at three crown positions (upper, middle and lower). From these measurements Ishii was able to propose his theory of foliage regeneration in *P. menziesii* with a particular focus on the role of epicormic sprouting. In the context of this theory, further analysis of Ishii's data is possible to continue to develop a picture of branch growth in old *P. menziesii*. In particular it is valuable to compare *P. menziesii* to a species that is similar, but does not exhibit proleptic reiteration. *A. grandis* was chosen in order to reveal the importance of the difference between the two species (Ford 2000), as well as how *A. grandis* can also persist with a different growth strategy.

Current Study

Further analysis is necessary to delineate and better characterize the concept of the SCU developed by Ishii and Ford (2001, Chapter I), and whether such an independent architectural unit exists. A quantification of the rules necessary to model branch growth and SCU formation in *P. menziesii* and observation of that growth over the lifespan of the branch would be key to understanding the role of reiteration in the growth of old *P. menziesii* branches, and whether there is a limitation to the renewal of foliage. This can most readily be accomplished through the development of an architectural computer simulation model (Chapter II), with accompanying field data.

Hinckley et al. (1998) suggest that the branch is a useful intermediate unit for scaling from the leaf level to the tree and stand levels, but the starting point for any inference is measurements made at the leaf level. Ishii used measurements of foliage mass, area and shoot demography in his description of branch growth in *P. menziesii*. With these measurements Ishii was able to delineate the foliage support system involved in the functional importance of epicormic sprouting and the reiteration of the SCU. For the purpose of this contrast it is thereby important to observe and describe the foliage support system utilized by branches of *A. grandis* through measurements of shoot demography, foliage area and foliage mass. To further understand the framework upon which each species holds its area and mass of foliage shoot length, length ratios and branching angles are also measured. This chapter addresses the analysis of these field data.

Foliage measurements

Specific needle area (SNA) has been shown to be positively correlated with net assimilation rate and nitrogen level per mass (Gower et al. 1993). SNA has also been shown to be positively correlated to relative growth rate in five evergreen conifers (Reich et al. 1998), and increased from the upper to lower crown in both *A. grandis* and *P. menziesii* (Kershaw and Maguire 1995), as well as other species (McLaughlin and Madgwick 1968; Ishii et al. 2002). Longer foliage longevity is also described as a characteristic of old trees (Bond 2000), and SNA was seen as inversely related to foliage longevity between species whose foliage longevity ranged from zero to eighty months (Gower et al. 1993). SNA has also been observed to decrease with increasing foliage age (Gholz et al. 1975, Smith et al. 1981; Hager and Sterba 1985; Borghetti et al. 1986; Bartelink 1996; Sprugel et al. 1996; Ishii et al. 2000). Differences in foliage longevity can result in different distributions of foliage along a branch axis in trees with similar basic architectural models (Fisher 1986). Takenaka (1994) used both SNA and a measure of the relationship between the length of a shoot and its foliage mass to simulate tree architecture. Therefore an analysis of the foliage area and mass of shoots of different ages is useful in a direct comparison of *P. menziesii* and *A. grandis*, which share a similar basic architectural model.

Architectural measurements

Both branching angles and relative lengths of branch parts have profound effects on the overall architecture of a branch or tree (Honda 1971). Honda and Fisher (1978, 1979) and Fisher and Honda (1979) found that observed values of the ratios of tree branch length and branching were close to values found, through simulation, to be optimal for effective leaf area display. Although the validity of such optimization exercises has been questioned (Fisher 1986, 1992), such analyses still imply the importance of branch angle and relative lengths in the display of foliage for a given species. Fisher (1986) also found that while clones grown in shade and sun did not differ significantly in branch angle and relative lengths of branch units, significant differences were found in leaf angle and absolute branch lengths. In the case of conifers with determinate growth, leaf angles correspond to branching angles of foliage-bearing shoots. These angles are thereby important in a plastic response to light conditions and subsequently light interception. Ford (1987) found that when he included an interference parameter in modeling plant growth, angle had a varying effect on growth. For a given maximum interference distance plant growth was maximized around 30^{o}. This also shows the importance of angle not only in foliage display, but also plant growth in relation to other plant parts. Kempf and Pickett (1981) compared angles and branch lengths of early and late-successional species, and found that early successional species had different properties than late. It is clear that branching angle and some measure of shoot length and relative lengths are important descriptions of plant architecture, and can be used to infer some kind of effective form of foliage display for a given species.

Site Description

The T.T. Munger Research Natural Area was established in 1934 to study old-growth Douglas-fir – western hemlock forests that were once common in Washington state (Ishii 2000). The natural area is located 45°49' N. latitude and 121°58' W. longitude, altitude 355 m (Franklin 1972). The stand is dominated by *P. menziesii* and *Tsuga heterophylla* (western hemlock), while *Thuja plicata* (western red cedar), *Abies amabalis* (Pacific silver fir) and *Taxis brevifolia* (Pacific yew) are also abundant. *A. grandis* and *Pinus monticola* (western white pine) are present in the stand (Ishii 2000). Franklin (1972) and Franklin and DeBell (1988) give a more complete description of the Wind River site.

Methods

Data for *A. grandis* and *P. menziesii* were collected in two ways. First, *A. grandis* branches were destructively sampled and measurements were taken similar to the destructive measurements described by Ishii and Ford (2001). Second, architectural characteristics were non-destructively measured from the Wind River Canopy Crane.

Destructive data gathered for A. grandis

It was decided that in order to make the most effective comparison, data similar to those gathered by Ishii for *P. menziesii* would be gathered for *A. grandis*. Therefore the study methods Ishii utilized were repeated here, but on a smaller scale (see Ishii 2000). As destructive sampling in the RNA is limited, permission was granted to harvest three branches, one each from three *A. grandis* trees. The trees were climbed in July 2001. An upper crown branch was taken from one tree, a middle crown branch from a second tree, and a lower crown branch from a third tree. Although this sampling method increased the possible causes of variation among the three branches (i.e. tree also becomes a causal factor), it was chosen to minimize the destructive impact on any one tree.

The branches were cut and lowered using ropes. On the ground the branches were labeled and then sectioned to facilitate transport. The foliated part of each branch section was covered with a plastic garbage bag and misted, and then the branches were driven to the University of Washington in Seattle (UW). They were stored in a cold room until they could be processed.

General branch measurements

In the laboratory the total length of each branch was measured and recorded. The branches were aged by counting the number of annual rings on a cross-section taken from the bottom of the branch. SCUs were then numbered and labeled. For this analysis the most basic definition of an SCU found in Ishii's work is used. Any foliated cluster of shoots that exhibited a main axis with 2-3 lateral branchlets per year that was spatially separated from other such clusters (through foliage death) was determined to be an independent SCU. The distance of the base of the SCU from the base of the branch was measured and recorded (hereafter "SCU position"), then the SCU was removed and the length and width of the foliated section were measured and recorded. The SCU was then stored in a Ziploc freezer bag in the cold room.

Shoot sampling

Foliated shoots were removed from each of the SCUs and sorted by shoot age. Three shoots from each age were sampled for foliage projected area measurements and the remaining shoots stored for foliage dry mass measurements. If there were fewer than six shoots in any given age class, all of the shoots were retained for projected area measurements. For both the sampled and remaining shoots the total length of the shoots placed end to end was measured and recorded. The foliage was then removed from the twigs for subsequent measurement. All needles were stored in the cold room until they could be measured.

Area and dry mass measurements

Projected leaf area was measured for all of the sampled shoots using the Optimas Image Analysis program. Needles were spread on a glass plate and sandwiched with another glass plate. A picture of the needles was taken and foliage area calculated by the Optimas program. If all needles of the sample could not fit on the glass plate, multiple measurements were taken and added together for a total area.

All needles were dried at 70° C until constant mass was reached, usually 2-3 days. The mass of both the sampled and remaining shoots for each age per SCU was measured and recorded.

Analysis of destructive data for A. grandis

This project is being treated as an exploratory data analysis for descriptive purposes, not for strict statistical tests. As such, significance was set at $\alpha=0.10$. All data were analyzed using the methods of linear regression and Analysis of Variance

(ANOVA; Neter et al. 1996). Table 3.1 lists all variables used in data analysis. Response variables were transformed when necessary to satisfy the requirements of regression (e.g. normality of residuals). For all analyses residual plots were created and analyzed for such assumptions. See Table C.1 for regression equations. In the case of needle dry mass per shoot length, piece-wise regression was used to determine the point at which the line changed slope (Neter et al. 1996). The breaking point was chosen as that which minimized the residual sums of squares in the model. The regression equation was taken from Neter et al (1996). In the case of categorical variables such as crown position dummy variable coding was used in regression predictions.

Specific needle area (SNA) of *A. grandis* for each age class in each SCU was calculated as the ratio of projected leaf area to leaf dry mass (cm^2/g). The total mass of each age class in each SCU was summed for the sampled and remaining shoots, and then divided by the sum of the shoot lengths in that age, yielding a mass of foliage per length of shoot for each age class (g/cm, hereafter termed mass per length). Predictor variables available for analysis were shoot age (0-11 years), crown position (upper, middle, lower: Ishii et al. 2000) and SCU position (distance from the base of SCU to base of the branch). These data were then compared to the data for *P. menziesii* obtained from H. Ishii.

Data analysis for P. menziesii

Data provided by H. Ishii (2000) for *P. menziesii* were also analyzed. Foliage mass per shoot was determined as an average across age and shoot type for shoots taken from three branches on each of two old-growth *P. menziesii* trees. The total dry leaf mass was divided by the total of shoot length for each age of shoot for both epicormic and regular shoots. The current year shoot was given an age of zero, last year's growth one and so on. These data as well as data for the SNA of *P. menziesii* were further analyzed as described above for *A. grandis*.

Non-destructive measurements: P. menziesii and A. grandis

In September of 2001, architectural branching data were collected from the Wind River Canopy Crane. Two *A. grandis* and two *P. menziesii* trees were chosen for measurement from within the crane circle. The live crown of each tree was divided equally into three crown positions: upper, middle and lower. One branch at each crown position was chosen for measurement. The height of each branch was approximated by the height of the gondola relative to the crane (hook height) at that branch. Starting from the deepest accessible foliated portion of the branch (i.e. the point closest to the trunk that could be reached by the crane), five SCUs were measured along the main axis of the branch. Of these, approximately every other branching node was measured along the main axis of the SCU. For each lateral shoot at that node the length of the lateral shoot, its parent shoot as well as the angle between them were measured and recorded (hereafter branching angle). This was repeated along the length of the lateral axis for all higher ordered shoots. The recorded shoot orders were with respect to the SCU, not the entire branching structure. Length ratios were calculated as the length of the daughter shoot divided by the length of the parent shoot (Figure 3.1) for all shoots of higher order than the parent (hereafter length ratio). This measurement was repeated for all shoots along the lateral axis of the whorl. The number of daughters for each shoot included both extension, lateral growth and epicormic growth. Each shoot was labeled as "epicormic" or “regular”. In addition, several epicormic sprouts ages one to seven were measured as above for each crown level of the two *P. menziesii* trees, with the exception of the upper crown of one of the trees.

Results

Detailed tables of analyses can be found in Appendix C. All significant regression lines found for each species are listed in Table 3.3 and Table 3.5. For comparative purposes the untransformed intercept of the variable is provided at each crown position. The intercept is calculated as the predicted value of the response variable when all of the other variables are set to zero. Forms of regression equations are given in Table C.1.

Destructive Sampling

General branch measurements for both A. grandis and P. menziesii

Table 3.2 gives general measurements of each branch for both species, including total number of shoots, total number of SCUs, shoots per SCU, proportions of SCUs in each developmental stage, branch age and branch length. Values for *P. menziesii* represent averages of three branches. For *A. grandis* the middle crown branch had the most SCUs, while the middle and lower crown branches had similar numbers of total shoots. Shoots per SCU were lowest in the middle crown, similar in the upper and lower crowns. Branch length increased from upper to lower crown, while percentage of epicormic shoots decreased from upper to lower crown.

P. menziesii branches were older and longer than *A. grandis* branches at all three crown positions (Table 3.2). The total number of SCUs was higher in *P. menziesii* in the upper and middle crown, while the total number of SCUs in the lower crown was similar in the two trees. Percentage of epicormic shoots was greater in *P. menziesii* at all three crown positions, as was the percentage of *P. menziesii* branches in epicormic initiation. More SCUs were in stages of decline in *A. grandis* than in *P. menziesii*.

General SCU measurements of A. grandis

There is a strong positive relationship between foliage length and foliage width of *A. grandis* SCUs (Figure 3.2). The linear trend is significant, with slopes close to one for each crown position (Table C.2). A second t-value was calculated to test whether the slopes were significantly different from one. The slope predicted for the upper crown branch was not significantly different from one ($p = 0.24$), the slopes of both the middle and lower crown branches were significantly less than one ($p=0.009$ and 0.023 respectively, Table C.2). This indicates that for the middle and lower crowns the foliage width for a given foliage length is smaller than the foliage length. Since intercepts of the regression lines for the upper and lower crowns were non-significant ($p = 0.62, 0.89$), regression was repeated setting the intercepts to zero (Table 3.3). This reduced the standard error and increased fits at all crown positions, and made the slope at the lower crown not significantly different from one (Table C.3). Given the almost one-to-one relationship between foliage length and width, length only was used in the remaining analysis.

As predictors of foliage length in *A. grandis*, both SCU age and crown position were significant ($p<0.001$), so the data were separated by crown position (Table C.4) and regression lines chosen for foliage length predicted by SCU age and SCU position. All crown positions showed positive regression lines (Table 3.3, Table C.5), indicating an increase in foliage length with SCU age. ANOVA shows SCU position also to be significant, either as a main effect or in an interaction with SCU age (Table C.4).

Specific Needle Area of A. grandis

SNA increased from the upper to the lower crown and decreased with increasing age of *A. grandis* (Figure 3.3). While in storage, parts of the lower crown branch had dried and had begun to lose needles before the SCUs could be fully processed. SCUs that had been labeled as dry were not included in the analysis. Crown position, shoot age and SCU position all significantly affected the log of SNA (Table C.6). A single linear regression equation was produced with crown position, age, SCU position and the interaction between age and SCU position, with crown position represented by a dummy variable coding. Figure 3.3 shows that the slope between ages zero and one is much steeper at all crown positions than between any other ages, so regression was repeated, once excluding age zero from the analysis. With SNA log transformed, the linear model excluding age zero shows a reduced residual sum of squares. Therefore the model that excluded age zero was used in predicting SNA. This regression equation showed SNA to be negatively related to both age and SCU position (Table 3.3).

Specific needle area of P. menziesii

SNA increases significantly from the upper to lower crown in *P. menziesii*, and there is a significant negative relationship between SNA and both shoot age and SCU position (Table 3.5; Figure 3.3, data from Ishii, also see Ishii 2002).

Comparison of SNA of A. grandis and P. menziesii

SNA was significantly lower in *A. grandis* than *P. menziesii* at all crown positions (Table 3.3; Table 3.5; Table C.7). Analyses were given both with and without the current-year shoots of *A. grandis* for the upper and lower crowns. There was a better regression fit obtained for leaf area when the current year was left out of the analysis for the upper and lower crowns of *A. grandis*. Table 3.4 shows that *P. menziesii* has both greater total mass and total foliage area per branch at each crown position. *A. grandis*, however, has greater foliage mass and area on regular shoots. The difference between the species lies in the totals for epicormic shoots (Table 3.4, Figure 3.4). When foliage area and mass are scaled by branch length the area per branch length for *A. grandis* is greater than *P. menziesii* in the upper crown, but that relationship is reversed in the middle and lower crowns (Figure 3.4b).

Foliage mass per shoot length of A. grandis

Foliage mass per length (g/cm) of *A. grandis* increased from approximately ages zero through three, then decreased from there for the upper and lower crown (Figure 3.5). There was a significant difference in foliage mass per length among the three crown positions, as well as in SCU position, shoot age, and the interactions of shoot age and SCU position with crown position. Normal residual assumptions were maintained in this case when the response variable was square root transformed. The data were then divided by crown position and piecewise linear regression produced at each crown level. In the upper crown the breaking point (i.e. age at which the shoot could be presumed to begin losing needles) was 1.25 years. In this case the response variable was log transformed to stabilize the variance. In the middle crown the breaking point was 1.5

years, and in the lower crown the breaking point was also 1.5 years. In both the middle and lower crowns a square root transformation was necessary. At all crown positions the parameters of the piecewise regression were linearly significant; SCU position was significant only in the middle crown. See Table 3.3 for final regression models.

Foliage mass per shoot length of P. menziesii

There is a slightly positive trend in foliage mass per shoot length of *P. menziesii* for approximately ages zero through four, then a strong negative trend approximately ages five plus (Figure 3.4, data from Ishii et al. 2002). The maximum longevity of foliage observed was eleven years, although the three shoots of that age had only negligible foliage biomass.

Piecewise regression relationships were predicted for each crown position. The breaking point in the upper and lower crowns was four years, while it was 4.75 years in the middle crown. At all crown positions a square root transformation was necessary to stabilize the variance. SCU position was significant only in the middle crown. See Table 3.5 for significant regression relationships.

Comparison of foliage mass per shoot length of A. grandis and P. menziesii

When all of the crown positions of *P. menziesii* and *A. grandis* are considered together there is a non-significant main effect of tree species on foliage mass per length (Table C.8). The data were square root transformed to stabilize the variance. Species did appear as significant in interactions with crown position and shoot age, indicating those two variables have different effects on foliage mass per shoot length in the two species. The intercepts of the regression equations predict *P. menziesii* to have a greater mass per shoot length when all other variables are zero, but this may be due to the significant interactions of tree species with the other predictor variables. On scatter plots (Figure 3.5) *A. grandis* appears to have greater mass per shoot length.

Non-destructive measurements

Length ratio between shoots of different order of both species

In *A. grandis* there was a significant negative relationship between ratio in length of lateral shoots to their parent and parent order when length ratio was log transformed in *A. grandis* (Table C.9). The length ratio was smaller on higher ordered shoots and was lowest in the upper crown (Table 3.3). Length ratio also decreased significantly with parent order in *P. menziesii* (Table 3.5). Length ratio was highest in the middle crown.

When the data for both species are analyzed together, species was significant in the species*crown position interaction (Table C.10). The three-way interaction of species*crown position*parent order was also significant. These interactions indicate that the effect of crown position is different between the two species.

Branching angle of both species

Branching angle in *A. grandis* was negatively related to both parent order and parent length (Table 3.3, Table C.11). In the linear regression model, the significant interaction between parent length and crown position compelled their inclusion as main effects, even though their regression parameters were seen to be non-significant ($p>0.10$).

In *P. menziesii* only crown position and parent length were seen to be significant predictors of branching angle. The regression equation showed parent length to be negatively related to branching angle (Table 3.5). When the data for both species are pooled together, *A. grandis* had a significantly higher average angle than *P. menziesii* across all crown positions (Table 3.6).

Epicormic sprouting in P. menziesii

In this study, the shoot that represents the first year of growth after a suppressed bud is released will be referred to as an initiated epicormic. On average in *P. menziesii*, initiated epicormics grow about 1.33 cm the first year. The second year of growth (or, the first daughter shoot of the initiated epicormic) averaged about 2.23 cm, a 68% increase from the first year. This increase in growth along the main axis continues into the next two years with an average length of 2.88 cm, a 29% increase from the second year, then an average length of 3.58, a 25% increase from the previous year. The third year of growth of the daughters of the initiated epicormic also seems to be the time at which the epicormic begins SCU formation. On average, the age at which lateral growth of the epicormic begins was 2.23, or between the third and fourth years of growth (ages two and three). This pattern is further illustrated by the average number of daughter shoots with increasing node number (where each shoot along the main axis is numbered beginning with one for the original epicormic shoot, i.e. the shoot whose bud had been released from dormancy). Node 1 had an average of one daughter shoot, with no variation from this value (not including those shoots which did not produce daughters, those were not measured). Node 2 had an average of 1.29 daughter shoots, while nodes

3-6 had averages of 1.82, 2, 2.5, 2.5 respectively (Figure 3.6(a)). Figure 3.6(b) is a map of a seven-year old epicormic shoot, illustrating this growth pattern. Table 3.7 gives general characteristics of initial epicormic shoot growth.

Discussion

General branch measurements

The comparison of general branch measurements of *P. menziesii* and *A. grandis* reflect their relative status in the forest stand. In terms of height *P. menziesii* dominates the stand. The major differences between the branches of these two species as summarized in Tables 3.2 and 3.4 lie in the total number of shoots and percentage epicormic shoots. *P. menziesii* has successfully renewed its foliage using epicormic reiteration, while *A. grandis* has not. Figure 3.4 shows that when epicormics are excluded from the total foliage mass and foliage area, *A. grandis* actually has both greater foliage and dry mass. Analysis of the effect of branching order would be another useful comparison that was unfortunately not possible here. Although *A. grandis* does not renew its foliage through epicormic sprouting, it may make up for that through higher ordered branching. Ishii observed the mean bifurcation ratio of lateral branchlets to be 2.35 in *A. grandis*, 1.44 in *P. menziesii*. In other words, *A. grandis* lateral shoots on average produce an extension and 1 1/3 lateral shoots per year, while *P. menziesii* lateral shoots produce an extension every year and one lateral shoot about every other year on average. Regardless of their relative status in this particular stand, however, *A. grandis* and *P. menziesii* do survive and coexist in the upper canopy of the WRCCRF.

Specific needle area of A. grandis and P. menziesii

As expected, SNA decreased from lower to upper crown in both species, indicating that needles of a given age in the upper crown have greater mass per area than do needles in the middle and lower crowns. This was also observed in loblolly pine (McLaughlin and Madgwick 1968), which the authors explained by different light conditions through the crown. In the lower crown, the higher SNA implies a greater light trapping surface per unit mass, implying needles that are adapted to the lower light conditions. A similar result for crown position was observed by Kershaw and Maguire (1995). Rio and Berg (1979) observed that in *P. menziesii* light level has a significant effect on SNA, with SNA decreasing with light level. In the current study SNA was also observed to decrease with the position of the SCU, such that SCUs further out from the base of the branch are predicted to have greater mass per area than those closer to the base of the branch. Sprugel et al. (1996) found that SNA in *Abies amabilis* (silver fir) was closely related to canopy openness, and suggest that SNA can be used as an index of light distribution within the tree canopy. Ishii (2000) observed a decrease in photosynthetically active radiation (PAR) down the crown of *P. menziesii* and *A. grandis* at the WRCCRF, and it is thereby possible that the changes in SNA vertically down the crown and horizontally along the branch axis of both species is due to light level.

SNA also decreased with increasing shoot age, implying that mass continues to increase throughout the life of the needle. Decreasing SNA with increasing shoot age has also been observed for different ages and different species (Smith et al. 1981; Hager and Sterba 1985; Borghetti et al. 1986; Ishii et al. 2002; Bartelink 1996; Sprugel et al. 1996, Gholz et al. 1975). Changes in needle mass as a shoot ages can be due to changes in starch levels (Smith et al. 1981). The large difference between current and one-year old shoots of *A. grandis* can be explained by the timing of sampling. Needles tend to gain mass as they mature due to cell wall thickening and starch accumulation (positive photosynthesis Kramer 1962). The *A. grandis* branches were harvested in the middle of the growing season (early July) and the needles were not yet mature. It seems that if the branches had been sampled later in the summer the difference in SNA between current and one-year old needles would not be so great. It was justified to not include current-year shoots in the regression analyses.

There were significant differences between the two species in SNA, with *A. grandis* exhibiting lower SNA at all three crown positions. SNA has been shown to be positively correlated to net assimilation rate (Gower et al. 1993) and relative growth rate (Reich et al. 1998).

Foliage mass per length of A. grandis and P. menziesii

The variable foliage mass per length is more subject to random error and noise than SNA due to its sensitivity to needle loss. The mass per length measurement is a factor of both the mass of individual needles as well as the number of needles per shoot. While individual needles are gaining mass with age, needles on the shoot may be lost, thereby decreasing the value of mass per length on any given shoot. This was observed for *A. grandis*. SNA for a given age class was unaffected by needle loss in branch processing because the remaining needles would still be representative of the SNA of the lost needles. In foliage mass per length, however, the measurement is dependent both on the mass and the number of needles on a given length of shoot. This is especially evident in the older age classes because these needles were already lost from the shoot before the branch was harvested. Needles from older age classes were more likely lost in the harvesting process and it may be that foliage mass per length is underestimated in the older age classes.

SCU position significantly affected foliage mass per length of *A. grandis* only in the middle crown. A possible explanation would be that light along the main axis of a branch in the middle crown of the tree may be more variable than in the lower or upper crowns. Further measurement would be necessary to investigate that claim.

The breaking points found to minimize the residual sums of squares of *A. grandis* indicate that needle loss begins between shoot age one and two at all crown positions. In other words, shoots of *A. grandis* begin to lose needles two to three years after the shoot is formed. In contrast, *P. menziesii* shoots lose needles at about age four at all crown positions. This indicates that *P. menziesii* holds onto its foliage longer over time, and thereby spatially along the main axis of its branching structure (Fisher 1986). That is, as a shoot ages potentially it becomes further removed from the terminus of the SCU as new shoots are grown. For both *A.* grandis and *P. menziesii* the process of foliage mass gain (as indicated by increasing SNA), which over time becomes offset by needle loss, is demonstrated by the positive slope for mass per length prior to the breaking point, then a negative slope for ages posterior to the breaking point.

Both SNA and the mass per length analyses indicate that the foliage mass on an *A. grandis* shoot would be greater than the mass of a *P. menziesii* shoot of same length. As Table 3.4 shows, however, *A. grandi*s still has lower total mass of foliage per branch.

Another comparison can be in leaf life-span; in *A. grandis* the oldest foliage-bearing shoot was ten years old, and that was at the lower crown. In the other two crown positions the oldest observed foliage-bearing shoot was seven years old, while for *P. menziesii* the oldest foliage bearing shoot observed at all crown positions was eleven years. Another indication of this is the breaking points reported above: at all crown positions *A. grandis* begins to lose foliage at a younger age than *P. menziesii*. In their discussion of the ecology of leaf life span, Chabot and Hicks (1982) outline several factors that may explain differential longevity of foliage. One major concept is a cost-benefit analysis, i.e. that the cost of producing a needle is paid off by that needle's contribution of new photosynthate. Another role of needles is storage of starch for future growth (Krueger and Trappe 1966); given that *A. grandis* needles are heavier, it may be that more starch is stored in the needles, so older needles are less necessary. For *P. menziesii* each needle may store less starch, but the presence of older needles allows for continued starch storage over time. Previous studies have shown that greater foliage longevity allows for a greater total foliage mass on a branch (Gower et al. 1993), but foliage longevity was observed to be inversely proportional to SNA (Gower et al. 1993) and relative growth rate (Reich et al. 1998). These results contradict what was found here, insofar as *P. menziesii* was observed to have both greater SNA and foliage longevity. The range of longevity in those studies, however, was from zero to eighty months. Relative to that scale the difference in longevity between *A. grandis* and *P. menziesii* is minimal, and therefore results relating longevity to other parameters may not be applicable here.

The fact that *P. menziesii* holds onto its foliage longer than *A. grandis* may also be a further indication of their contrasting branching strategies. Analogous to epicormic sprouting, in which foliage is regenerated along the main axis of the branching structure, a higher foliage longevity also helps to maintain an inner crown in *P. menziesii*. *A. grandis*, however, invests heavily in current foliage (with a greater mass) that falls off more quickly, but foliage may then be regenerated through high bifurcation along the terminus of the main and lateral axes of *A. grandis*. Fisher (1986) stated that foliage distribution along an axis may vary while axis position remains unchanged through a mechanism such as different foliage longevity.

Length ratio and branching angle

The ratio between the length of a lateral shoot and its parent in both *A. grandis* and *P. menziesii* was significantly influenced by the order of the parent shoot. In both cases, parent order had a negative influence on the length ratio, such that the ratio in lengths between a first and second order shoot was higher than the ratio in lengths between a second and third order shoot. Length ratios were also seen to be significantly different between the two species; average values across parent order between the two species appear similar in the upper crown and in the middle and lower crowns *P. menziesii* has higher average length ratios (Table 3.6). The decrease in length ratio with higher shoot order is not unexpected. This results from the dominance of the apical meristem, and has been widely observed (see Wilson 2000). Several explanations have been proposed, including hormonal control of the apical meristem, a reduction in hydraulic conductivity between terminal and lateral shoots, particularly at the junction between them (Zimmerman 1978, Borchert and Honda 1984), and a competition between shoots for water and nutrients that is dominated by the apical meristem (Moorby and Wareing 1963), thereby reducing growth in lateral shoots relative to terminal ones.

Branch angles also differed significantly between the two species. Although the branching angle of both species was observed to be negatively related to parent length, branching angle was negatively related to parent order in *A. grandis* only. At higher orders of branching in *A. grandis* the angle becomes less, i.e. as order increases the foliage becomes more tightly packed. This may not have been significant in *P. menziesii* because higher orders were rarely observed. Fisher and Honda (1977, 1979) observed length ratios and angles that were near optimal for efficient foliage display in a tropical species. While such optimization studies may not be biologically valid (Farnsworth and Niklas 1995; Fisher 1986), they can be instructive if taken in appropriate contrast. It may be that the differences in length ratio and branching angle observed in *P. menziesii* and *A. grandis* represent two different solutions to the problem of growth and survival in an old-growth canopy.

Summary

These data reveal clear differences in the process of foliage growth and regeneration in *P. menziesii* and *A. grandis*. Epicormic sprouting is important to the survival of *P. menziesii* branches, especially when seen in relation to the growth of *A. grandis*. Without epicormic growth *P. menziesii* would have much less photosynthetic organs on its branch. *A. grandis* has a more conservative approach with shorter branches, and it holds almost all of its foliage on regular shoots. It regenerates its foliage through regular growth, possibly through continued bifurcations in higher ordered shoots. The bifurcation of *P. menziesii* seems more limited, but it makes up for that through regeneration of epicormic shoots. *A. grandis* also has more foliage mass per projected leaf area (lower SNA) at all crown positions and shoot ages. Architectural data also show differences between the two species. This analysis implies that although superficially *A. grandis* and *P. menziesii* have similar basic architectural models, small modifications in those models have led to significantly different growth characteristics. A simulation model can explore those differences in more detail throughout the development of the branching structure.

Table 3.1: Variables used in data analysis

Variable	Abbreviation	units	Description
crown position	crown.pos	none	divide crown into 3 approximately equal sections, upper, middle and lower
species	spp	none	indicates species studied, where 1=*P. menziesii*, 2 = *A. grandis*
length ratio	lrat	none	a measure of the length relationship between a shoot and its lateral daughter shoot (see Fig. 1.2)
branching angle	angle	degrees	a measure of the angle between a shoot and its lateral daughter shoot (see Fig. 1.2)
parent	none	none	the parent shoot of the shoot of interest
shoot order	shoot.ord par.ord	none	the order of the shoot relative to the main axis of the SCU, where lateral shoots have order 1 greater than their parent shoot
foliage length	fol.len	cm	length of the foliated section of the SCU
foliage width	fol.width	cm	width of the widest foliated section of the SCU
SCU position	dist.out	cm	distance from the base of the SCU to the base of the branch
shoot age	age	years	current shoots are age 0, then one year old and so on
specific needle area	SNA	cm^2/g	ratio of projected needle area to needle dry mass, calculated for a sample of shoots in each age class
mass per shoot length	wt.l	g/cm mg/cm	a measure of the dry mass of needles on a shoot divided by the length of the shoot

Table 3.2: General branch measurements for *A. grandis* and average values for *P. menziesii* (from Ishii, 2001)

tree	*A. grandis*			*P. menziesii*		
Crown position	Upper crown	Middle crown	Lower crown	Upper crown	Middle crown	Lower crown
Branch age (years)	11	39	63	89.7	147.7	94.3
Branch length (m)	1.51	3.7	4.04	3.57	6.37	2.83
Total number of SCUs	8	87	38	32.7	119.7	36.3
Total number of Shoots	676	2702	2858	4140.7	15438.7	4860.7
% epicormic shoots	17.3	6.3	0.68	20.7	30.0	42.6
Shoots per SCU	113	31	105	126.6	128.98	133.3
% SCUs regular growth	25	24.1	7.9	21.8	3.7	1.33
% SCUs decline 1	0	66.7	68	5	13.3	7
% SCUs epicormic initation	12.5	4.6	2.6	46.33	27	27
% SCUs decline 2	37.5	4.6	0	3.7	26.7	22.3
% SCUs unknown stage	25	0	21.1	0	0	0

Table 3.3: Significant regression relationships for *A. grandis*

Response Variable	Crown position	Regression equation	Untransformed intercept
Foliage length$_{\mathrm{SCU}}$	upper	fol.len$_{\mathrm{SCU}}$ = 1.02*foliage width$_{\mathrm{SCU}}$	NA
	middle	fol.len$_{\mathrm{SCU}}$ = 0.933*foliage width$_{\mathrm{SCU}}$	NA
	lower	fol.len$_{\mathrm{SCU}}$ = 1.05*foliage width$_{\mathrm{SCU}}$	NA
	upper	fol.len$_{\mathrm{SCU}}$ = -1.69+6.59*SCU age	NA
	middle	fol.len$_{\mathrm{SCU}}$ = 11.91+1.86*SCU age	NA
	lower	fol.len$_{\mathrm{SCU}}$ = 23.64+0.878*SCU age	NA
log(SNA)	upper	3.7760 - 0.0443* age - 0.000668*SCU position + 0.0000987*age*SCU position	43.64
	middle	4.1077 - 0.0443*age - 0.000668*SCU position + 0.0000987*age*SCU position	60.81
	lower	4.2244 - 0.0443* age - 0.000668*SCU position + 0.0000987*age*SCU position	68.33
mass per length$_{\mathrm{shoot}}$ (mg/cm)	upper	wt.l$_{\mathrm{shoot}}$ = (3.69+1.05*age-1.23*(age-1.25)*X)^2 X = 0 for age$\leq$1.25, 1 otherwise	13.62
	middle	wt.l$_{\mathrm{shoot}}$ = (5.78+1.27*age-3.26*(age-1.5)*X+0.0043*SCUposition)^2 X = 0 for age$\leq$1.5, 1 otherwise	33.41
	lower	wt.l$_{\mathrm{shoot}}$ = (4.67+1.58*age-2.03*(age-1.5)*X)^2 X = 0 for age$\leq$1.5, 1 otherwise	21.81
length ratio of higher order shoots	upper	log(lrat) = -0.2178-0.0462*parent order	0.8043
	middle	log(lrat) = -0.1249-0.0462*parent order	0.8826
	lower	log(lrat) = -0.1271-0.0462*parent order	0.8806
branching angle	upper	angle=57.7679-1.472*parent order+0.4859*parent length	57.77
	middle	angle=60.34-1.472*parent order-0.1802*parent length	60.34
	lower	angle=67.7349-1.472*parent order-1.2426*parent length	67.73

Table 3.4: Total foliage area and dry mass of each *A. grandis* branch and average values for *P. menziesii* at the three crown positions. The "without epicormic" totals include only SCUs not of epicormic origin.

Tree Type	epicormics?	crown position	foliage dry mass (kg)	area (m^2)
A. grandis	with epicormics	upper	0.555	2.37
		middle	0.692	4.02
		lower	0.408	2.06
	without epicormics	upper	0.461	2.02
		middle	0.540	3.11
		lower	0.378	1.88
P. menziesii	with epicormics	upper	0.942	4.52
		middle	3.247	19.88
		lower	0.708	5.16
	without epicormics	upper	0.101	0.518
		middle	0.070	0.406
		lower	0.027	0.215

Table 3.5: Significant regression relationships for *P. menziesii*.

Response Variable	Crown position	Regression equation	Untransformed intercept
SNA	upper	sqrt(SNA) = 7.5715 - 0.1611*age - 0.0010*SCU position + 0.00001985922*age*SCU position	57.33
	middle	sqrt(SNA) = 8.7034 - 0.1611*age - 0.0010* SCU position + 0.00001985922*age* SCU position	75.75
	lower	sqrt(SNA) = 9.0927 -0.1611*age - 0.0010* SCU position + 0.00001985922*age* SCU position	82.68
mass per $\text{length}_{\text{shoot}}$ (mg/cm)	upper	$\text{wt.l}_{\text{shoot}}$ = $(8.1743+.03203*\text{age}-1.7214*(\text{age}-4.0)X)^2$ X=0 for age≤4, 1 otherwise	66.82
	middle	$\text{wt.l}_{\text{shoot}}$ = $(7.1148+0.1948*\text{age}-1.3494*(\text{age}-4.75)X)^2$ X=0 for age≤4.75, 1 otherwise	50.62
	lower	$\text{wt.l}_{\text{shoot}}$ = $(5.9332+0.0346*\text{age}-0.8801*(\text{age}-4.0)X)^2$ X=0 for age≤4, 1 otherwise	35.20
length ratio of higher ordered shoots	upper	length ratio = 0.8654 - 0.0807*parent order	0.8654
	middle	length ratio = 1.1261 - 0.1717*parent order	1.1261
	lower	length ratio = 0.8644 - 0.0021*parent order	0.8644
Branching angle	upper	angle = 61.2467-1.2327*parent length	61.25
	middle	angle = 58.9524-1.2327*parent length	58.95
	lower	angle = 61.3765-1.2327*parent length	61.38

Table 3.6: Average length ratio and angle values at three crown positions for *A. grandis* and *P. menziesii*

tree	*A. grandis*			*P. menziesii*		
crown position	upper	middle	lower	upper	middle	lower
average length ratio	0.772	0.786	0.802	0.756	0.901	0.861
average angle	58.59	56.81	57.90	56.38	54.14	55.73

Table 3.7: General characteristics of initial epicormic shoot growth in *P. menziesii*.

Variable	Average values
age at lateral growth	2.25 years
initial length	1.33 cm
first year length	2.23 cm
second year length	2.88 cm
third year length*	3.58 cm
Number of shoots**	
Node 1	1
Node 2	1.29
Node 3	1.82
Node 4	2
Node 5	2.5
Node 6	2.5

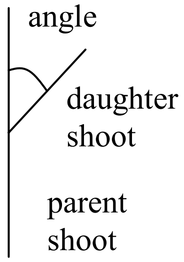
* There are fewer data points for the third year length average.

** Successive nodes have decreasing data points

$$\text{length ratio} = \frac{length_{daughter}}{length_{parent}}$$

a)

branching angle=



b)

Figure 3.1: Explanation of length ratio and branching angles

a) Equation for calculation of length ratio.
b) Illustration of terms used in field work, and definition of branching angle.

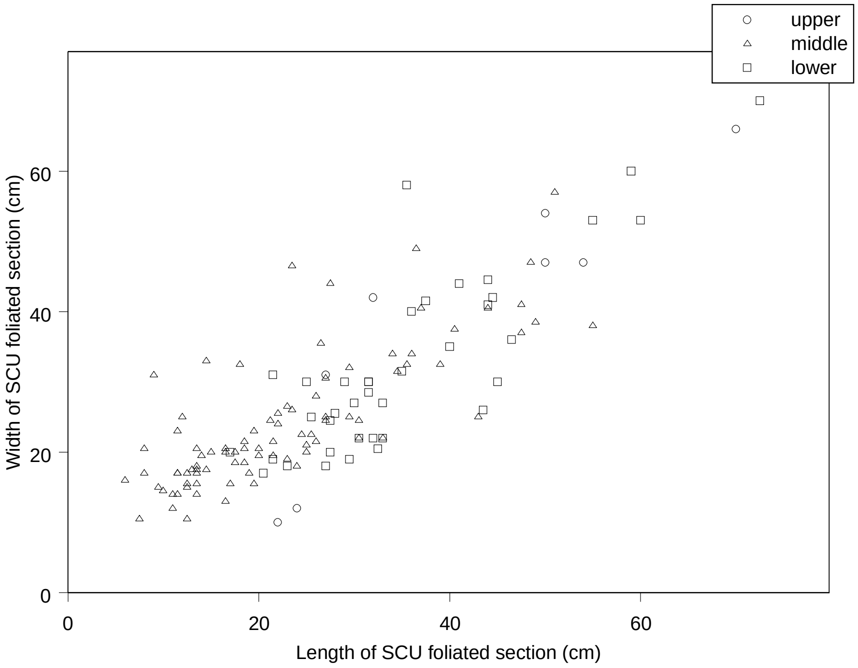


Fig. 3.2: Relationship between SCU foliage length and width in *A. grandis*. There is a 1-1 relationship across all crown positions.

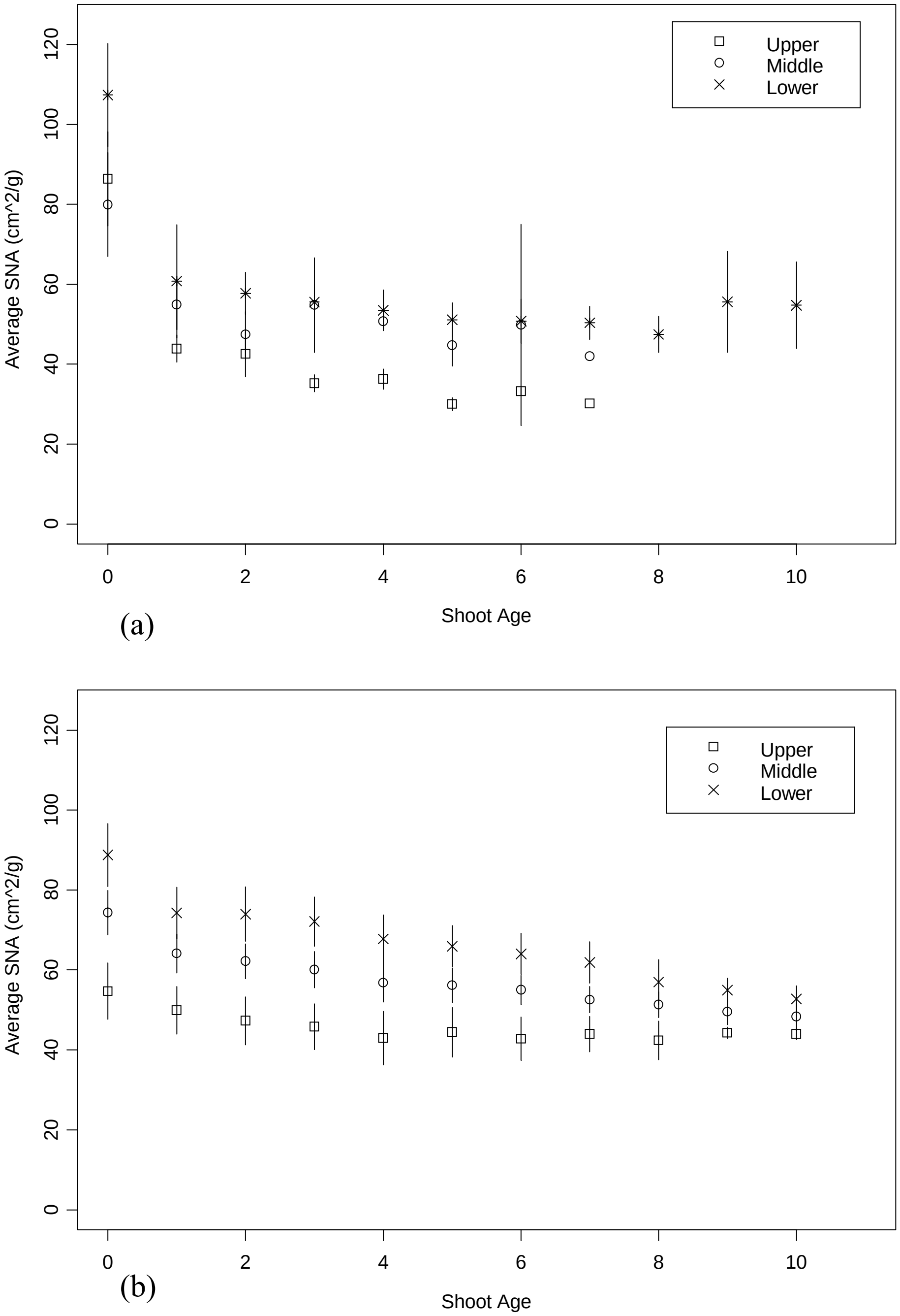


Fig. 3.3: Average SNA decreases with shoot age and increases from the upper to lower crown in (a) *A. grandis* and (b) *P. menziesii*. Vertical lines represent +/- one standard deviation from the mean.

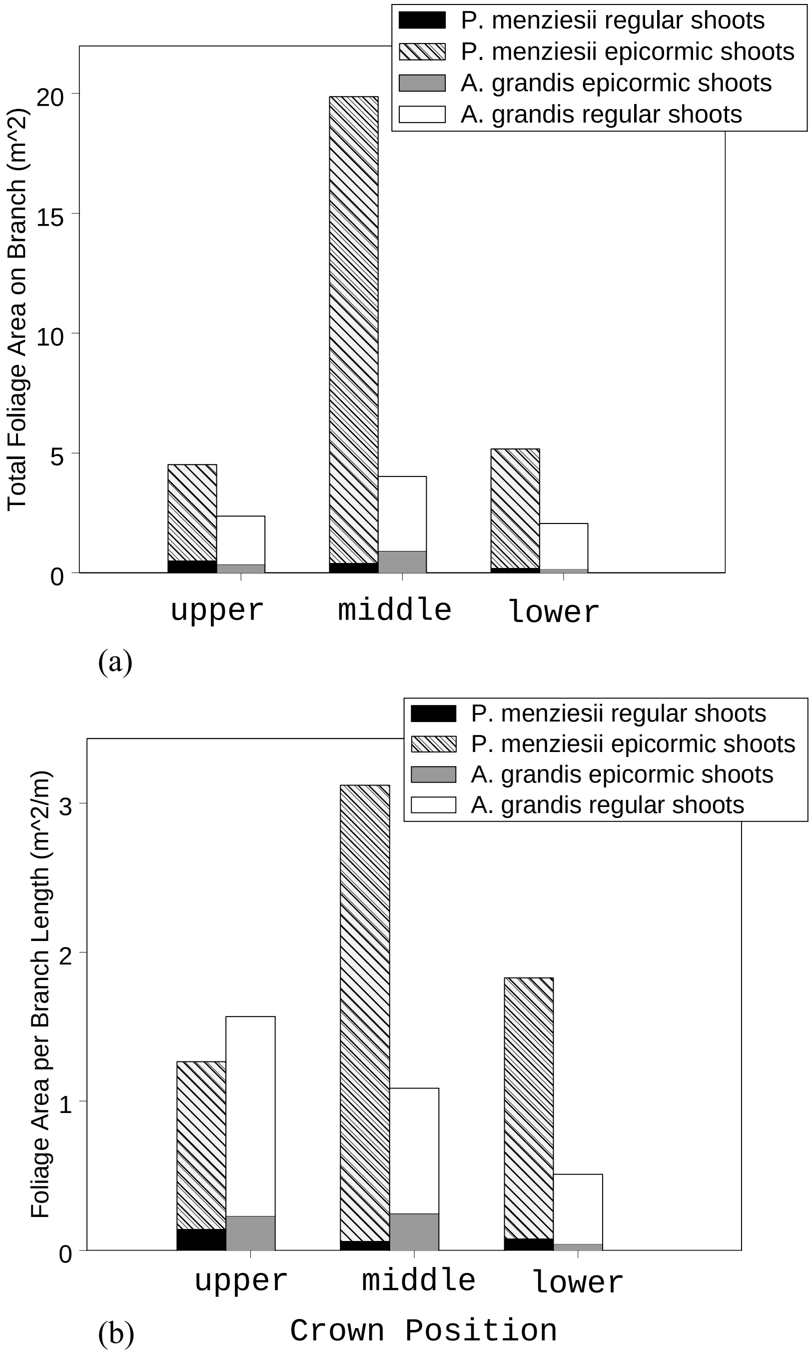
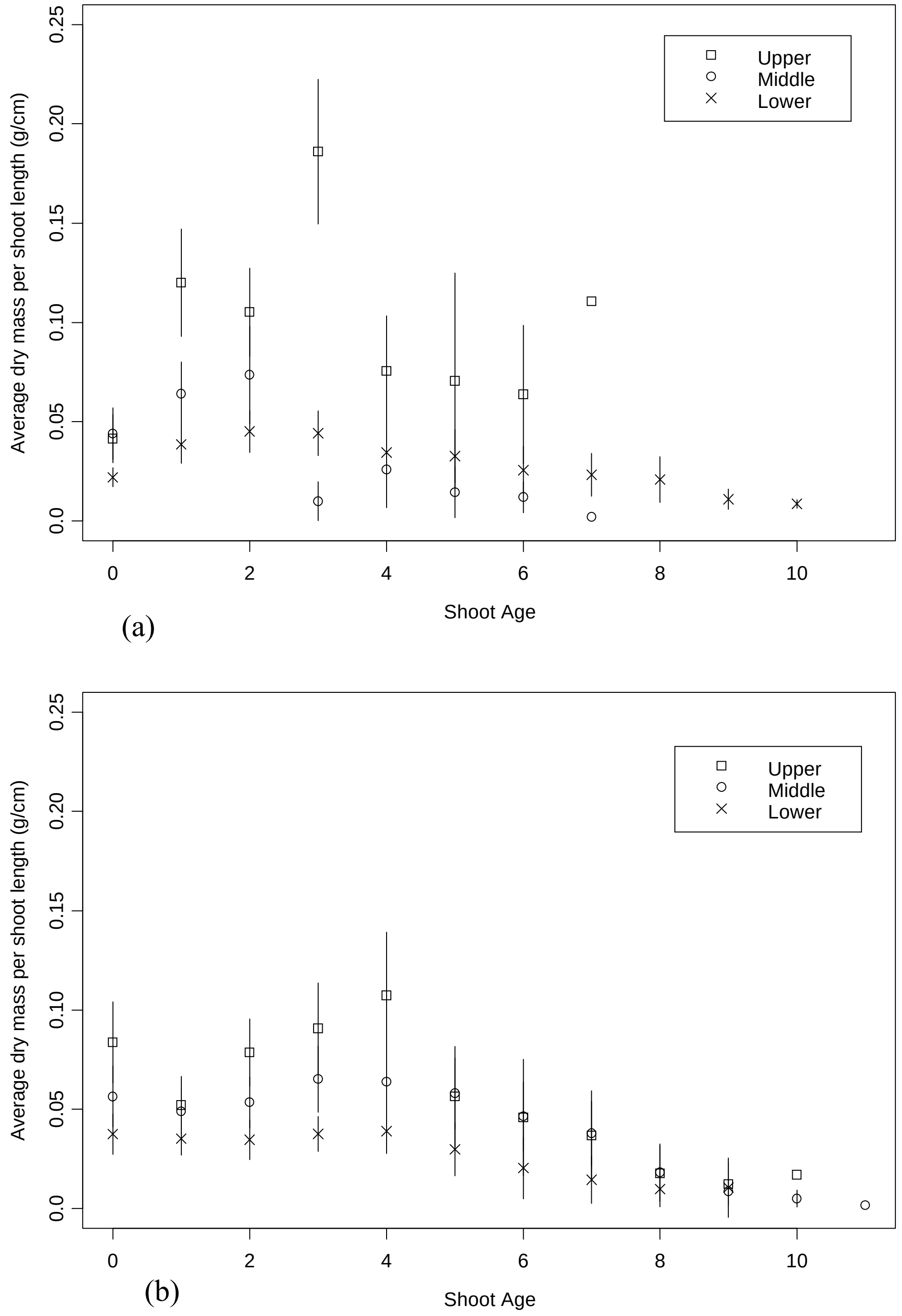


Figure 3.4: Foliage area for branches of *A. grandis* and *P. menziesii*.

a) Foliage area per branch of *P. menziesii* and *A. grandis* at three crown positions. A similar relationship is found with foliage mass.
b) Foliage area per length of branch (m^2/m).



(a)

(b)

Fig. 3.5: Average foliage dry mass per shoot length at three crown positions for (a) *A. grandis* and (b) *P. menziesii*.

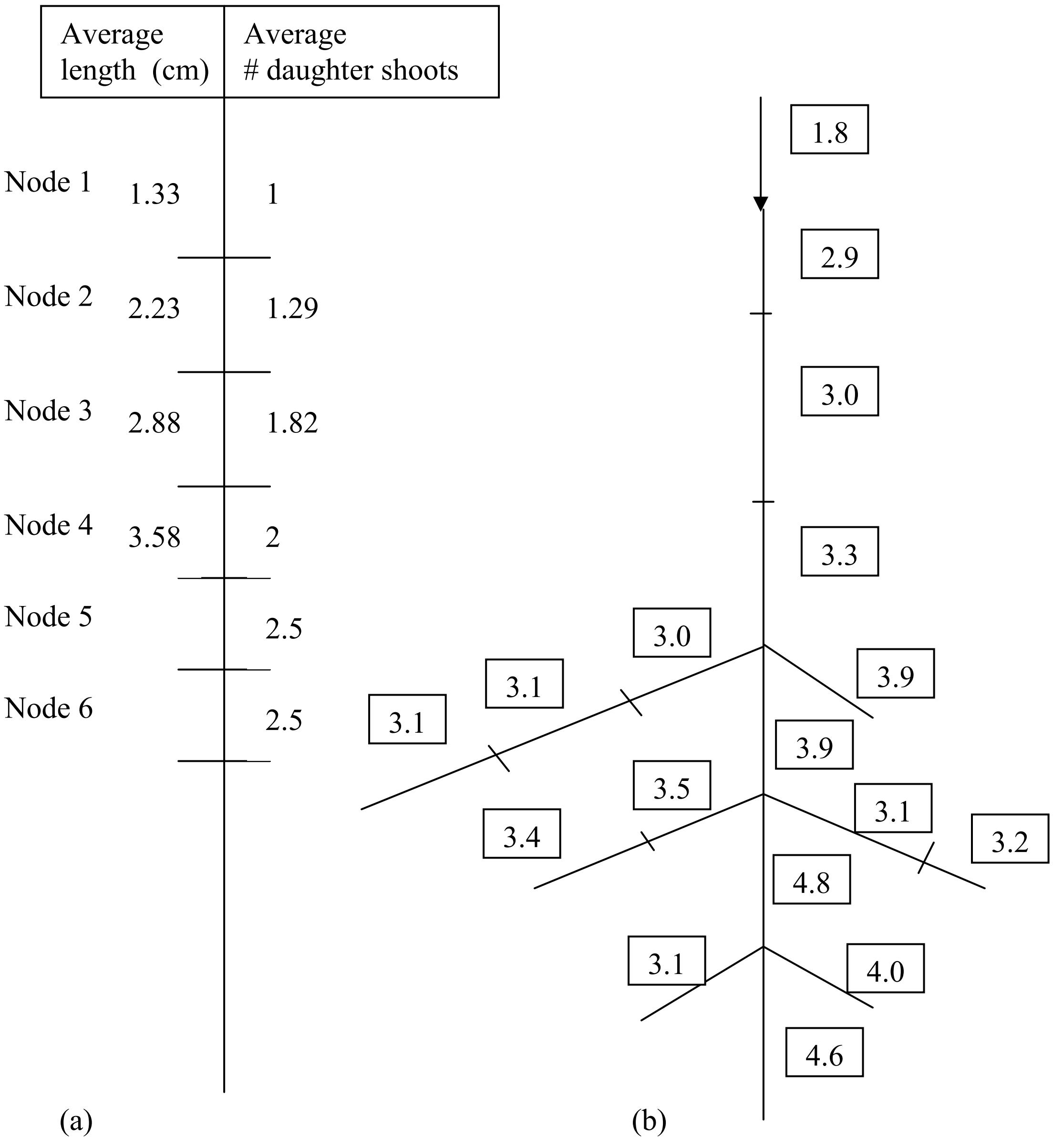


Figure 3.6: Growth of a newly forming SCU in *P. menziesii*.
a) Schematic of the main axis of a newly forming SCU, with average lengths and number of daughter shoots shown. Segments are numbered by node, with one being the first epicormic shoot.
b) Map of a typical young epicormic shoot in *P. menziesii*, demonstrating limited growth and expansion during the first few years, then exhibiting the characteristics of SCU growth between years three and four. Numbers in boxes are shoot length (cm), map not to scale.

Chapter IV

Geometric computer simulations reveal limitation on branch complexity

Introduction

It has been demonstrated that basic branching forms of trees can be characterized and produced through the variation of a few simple parameters including length, branching angle, and bifurcation ratios (Honda 1971). From these parameters more complex relationships between branch form and growth can be studied, including foliage area display and the distribution of foliage along a branching axis (Honda and Fisher 1979; Tomlinson 1983; Bell et al. 1979). Modeling exercises are useful in inferring the architectural consequences of particular geometric rules, which in the field would be very difficult (Room et al. 1996; Prusiskiewicz 1998; Fisher 1992). Many of the modeling exercises that have been performed are limited in space and time (usually up through thirty years), and there has not been a computer simulation that incorporated reiteration (Tomlinson 1983; Fisher and Honda 1977). This study integrates a simple architectural model of branch form with the reiteration of basic branching units in order to better understand branch survival in an old-growth forest. Basic model development is described in Chapter II.

Bifurcation Ratios

Fisher and Honda (1977) explored changes in the efficiency of foliage surface area with increasing bifurcation ratio. They found that although total leaf area increased with increasing bifurcation, the efficiency of the leaf area decreased. They believe that natural limitations on bifurcation increase the efficiency of leaf surface on a branch.

Borchert and Honda (1984) found that hydraulic flux decreased with high branch order and that high bifurcation with increasing branch order gave unrealistically dense trees. A natural decrease in bifurcation with increasing order was due to an exponential decrease in the hydraulic flux of lateral branches with increasing order. These above results justify the use of bifurcations explored across the branching system and the effect of those bifurcations on growth of the branch. Bifurcation ratios are central to the analysis of the current geometric branching model. In the modeling analysis it was assumed that bifurcation ratio would decrease with increasing branch order, as was previously observed. While other descriptors of growth were also observed to be important in determining branch form of different species (such as growth rates, length ratios between shoots of higher order, foliage longevity, foliage area, branching angles), these were not analyzed in the current study and were taken to be constants determined by the data analysis in Chapter III (Tables 3.3 & 3.5). In general, as a branch ages its position in the crown of the tree also changes. Therefore, as the simulated branch ages the values of the constants shift to those determined by data from each of the crown positions (upper, middle and lower). The age at which the transition occurs was determined by the branch ages observed at each crown position (Table 4.1).

There are several questions that this modeling exercise can address. What is the influence of reiteration on growth? It may be that reiteration is a minor part of a larger branch system, or that it is the major driving force behind branch growth. Given that reiteration occurs, what is its limit? Theoretically a branch that avoids catastrophic damage could continue to rejuvenate its foliage through proleptic reiteration ad infinitum.

In the absence of reiteration, how can a branch maintain its foliage? These questions are addressed in this chapter.

Methods

Preliminary model runs

The simulation model analysis proceeded in several steps. Preliminary model runs were performed to assess the overall execution of the model. As an initial indicator of model performance, total live shoots on the branch was plotted over time for each model run and then compared at different years to the total live shoots observed for each species. In this preliminary analysis the simulation model was first assessed for stochastic effects by utilizing a random number generator that required whole integer seed values. This allowed for a systematic exploration of different seed values, and the developmental differences that accounted for the variability of model outputs with the same bifurcation ratios. A population of 50 model runs was produced using seed values 1, 2, 3, …, 50. These runs were analyzed and six integer seeds that yielded the range of model outputs were chosen for detailed developmental analysis. If the variability in model outputs was deemed unrealistic, the model was modified accordingly until satisfactory ranges were achieved. To save computation time for all analyses, the simulation was aborted after the next year's growth if total shoots became greater than 200,000.

Sensitivity analysis

The model was assessed for its sensitivity to changes in bifurcation ratios at three orders of branching. For each species a local sensitivity analysis was performed in conjunction with factor screening (Campolongo et al. 2000). In the local sensitivity analysis the average bifurcations for each order were changed individually, while the others were held constant. In a factor screening different factors are run in their possible combinations and the outputs compared. In this simulation model there are two factors: rules for epicormic initiation (three rules) and SCU independence (two rules). These two factors have six distinct combinations (Table 4.2) and the local sensitivity analysis was attempted for each of the six rule combinations. For *A. grandis* the different rules for epicormic initiation were not explored because epicormics were assumed to make a negligible contribution to growth, leaving only two possible rule combinations for *A. grandis*.

In the sensitivity analysis the model was first run with the default parameter set, which was determined by preliminary analyses (Table 4.1, Table 4.2). Drawing values for first order bifurcation from a uniform distribution and keeping the other bifurcations at their default values generated twenty more parameter sets. The limits of the uniform distribution were set from zero to three in *P. menziesii*, the limits of daughter shoots allowed for in the model (Table 4.3). Slightly increased ranges were explored for *A.* grandis (zero to four). When sampling of first order bifurcation was complete, the parameter was reset to its default value. This sampling procedure was repeated for second and third order bifurcations and the average bifurcation of newly initiated epicormic shoots, yielding a total of eighty parameter sets for each rule combination.

For the sensitivity analysis the same random seed was used for each parameter set. This controlled for stochastic effects and all observations were then based on changes in the parameter values. A random seed integer that yielded a central value in the population of 50 model outputs was chosen for use throughout the sensitivity analysis (seed = 21,17 for *P. menziesii* and *A. grandis*, respectively). Analyses were repeated for each species, and to save computation time the model was run for ninety years for both species. The sampled bifurcation ratios were plotted against their corresponding total live shoots at year ninety to infer the effect of increasing bifurcation at each branch order on shoot growth.

Long model runs

In additional to sensitivity analysis the model was run for four hundred years at the default parameter values for each species and model behavior over this time period was observed (Figure 4.1). If the branch died before four hundred years, the run was terminated and that year was recorded as the terminal age of the branch. Five integer seeds were run for each species to assess stochastic effects in the long-term pattern of growth. In addition, a population of fifty branches was produced for both species and frequency histograms of terminal age of the branch were plotted. Finally, the dynamics of SCU formation in *P. menziesii* throughout the development of the branch was explored.

Results and Discussion

Preliminary model runs: P. menziesii

Plots of total live shoots over time reveal highly variable model outputs for the population of 50 model runs with the same parameter values (see Table 4.1). Total live shoots for these populations at year ninety range from zero to 18,621 (Figure 4.1). A zero result indicates that at some time before year ninety mortality was greater than bifurcation and the number of live shoots on the branch declined to zero. The year at which that occurred will be referred to as “terminal age.” Branches in only eleven of the fifty runs grew up to ninety years and the youngest terminal age of a branch was eighteen years.

This variability in the model outputs is unrealistic with respect to what was observed for *P. menziesii*. The average number of shoots observed around age ninety for *P. menziesii* branches was 4140, and 18,621 shoots at year ninety seems to be an impossibly large number. Also, given that the goal of this project is to observe the growth of long-lived branches, it is unreasonable to allow branches to die at eighteen years. Borchert and Slade (1981) speculated that while geometric models with simple rules could produce reasonable branch forms over the short term, cumulative effects caused high variability over the long-term. The results of the preliminary model runs described above demonstrate such high variability, indicating that the basic model described in Chapter II is inadequate in this context. Some kind of upper and lower bounds on shoot growth must be included in the simulation to account for the observed cumulative effects.

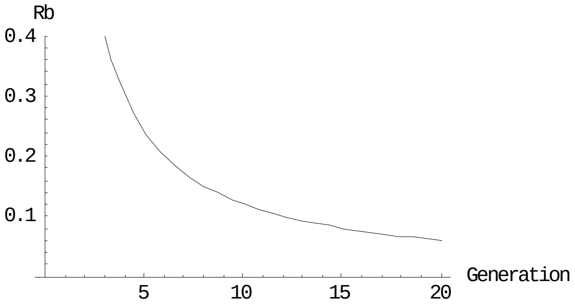
In the population of 50 branches, random number sequences that resulted in the loss of the regular main axis of the branch within the first 20-30 years (i.e. the first order regular shoot drew a zero from the Poisson distribution) were more likely to have their total shoots reach zero before the end of the model run. In order to further differentiate the characteristics that most influenced the stochastic variability, six integer seeds that yielded the range of observed model outputs were chosen for more detailed analysis (Table 4.1). Plots of total live shoots as well as total live epicormic shoots over time for the six model runs were generated over both ninety and fifty years (Figure 4.2). The total live regular shoots show almost identical patterns through forty years of growth: a period of expanding growth, a peak and then a decline. The main difference among the model runs lies in the pattern of epicormic shoot growth; the number of epicormic shoots was never higher than ten for runs that reached zero live shoots at year ninety. In those cases, when the regular main axis is lost there are no first order shoots generated via proleptic reiteration. However, in model runs in which there is successful epicormic sprouting and subsequent establishment of new SCUs, the total live shoots increase throughout the time period of the model run (Figure 4.2). To prevent the premature death of a simulated branch, the model was modified to deterministically allocate three daughter shoots each year to the terminal node of the regular main axis. Year fifty was defined as a starting point at which the main axis first becomes subject to the random Poisson process. This lower bound on growth should provide all branches sufficient opportunity for the establishment of epicormic SCUs before the regular main axis is lost.

With the addition of a tighter lower bound, end total live shoots are still highly variable (Figure 4.1(b)). The low average bifurcation assigned to a newly initiated epicormic shoot (around 0.70) explains the variability observed in the successful growth of new SCUs. This bifurcation is assigned because higher values consistently result in unrealistic total numbers of live shoots. A low average bifurcation for new epicormic shoots results in the possibility that no epicormic axis firmly establishes itself over the first few decades of growth. On the contrary, if several newly sprouted epicormic shoots along the regular main axis are established and result in new SCUs, then the framework is laid for a tremendously high rate of growth. This pattern was observed with the result of 25,332 total live shoots at year ninety.

Halle et al. (1978) observed a decrease in growth of the reiterative complex of tropical species as the number of complexes increase. This decrease included the size of the complex as well as fewer branches and internodes. While they were referring to reiteration of vertical tree complexes, it would seem that a similar reduction applies to the case of horizontal reiterated complexes such as the SCU in *P. menziesii*. The highest epicormic generation that Ishii and Ford (2001) observed was seven, while the model runs that had the highest total shoots at year ninety had up to fourteen generations of epicormic shoots. Therefore a reduction of growth of the reiterated complexes with increasing generation number is a reasonable upper bound on branch growth in the simulation model.

There is no theoretical basis for reducing growth of reiterated complexes with increasing generation. It was decided that the simplest method in the context of the current simulation model was a continuous reduction in the average bifurcation ratio of first order epicormic shoots with increasing generation. A function was chosen in which the average bifurcation ratio was assumed to be constant through the first three generations, then was inversely proportional to the epicormic generation:

$$Rb_{red} = Rb_{ini} \times \frac{3}{epi_{gen}};$$

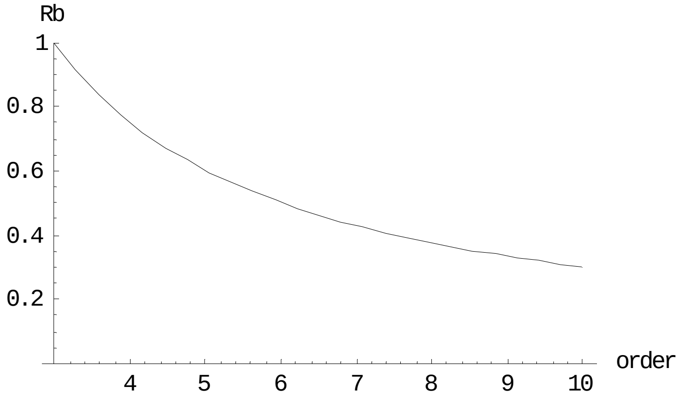


Rb_{ini} is the parameter value for the average bifurcation for the first two years of growth of a newly sprouted epicormic. The variation in total shoots over time was successfully narrowed by this growth limitation (Figure 4.1(c)). The equation can be modified according to the generation at which the reduction is to take place, i.e. replace the three with a four if the reduction is to take place at generation 4.

Preliminary model runs A. grandis

Default parameter values chosen for *A. grandis* are given in Table 4.2. The lower bound on growth established above for *P. menziesii* is also used in the simulation of *A. grandis* branches. The total number of live shoots ranged from 509 to 7454 for the population of 50 branches (Figure 4.3). The lower bound of 500 shoots is a reasonable number of shoots at year ninety, yet 8000 shoots is almost twice the maximum number of shoots observed for a sixty-year-old branch. In this preliminary simulation shoots of order three and higher are assumed to have equal bifurcations; this assumption is probably unrealistic, as bifurcation is observed to decrease with increasing shoot order. To prevent the need for separate parameters for each shoot order greater than three a continuous function is used to reduce bifurcation with increasing order:

$$Rb_{red} = Rb_3 \times \frac{3}{shoot_{order}};$$



This function is similar to that used above to restrict growth of SCUs with increasing generation. With this reduction in average bifurcation with increasing order the range of stochastic outputs became zero to 932. Since the oldest observed branch was 63, it is possible that *A. grandis* branches die at year ninety, and one thousand shoots is also reasonable at that year. This growth reduction was kept for subsequent simulations of both species.

Summary of Preliminary Analysis

Although branch growth has been shown to differ between *A. grandis* and *P. menziesii*, it is clear that a similar limitation on growth spatially through the branch structure is a necessary upper bound on growth. The character of that limitation reflects the contrast between the two species; for *P. menziesii* it is sufficient to restrict growth with increasing epicormic generation, while for *A. grandis* the restriction must be for increasing order. The common element in those restrictions is a limitation on the complexity of the branch. This is obviously correlated with age, since as a branch ages it also increases in complexity. In the long model runs described below the relationship between complexity and age will be further explored. Another contrast between the two species is in the default parameter values used. If the default values established for *P.*

menziesii were applied to *A. grandis* the majority of the *A. grandis* branches would have died before the end of the model run. It is clear that in the absence of proleptic reiteration *A. grandis* must utilize higher bifurcations across the first three orders of branching.

***P. menziesii* sensitivity analysis**

Rule Combination 1 (Table 4.2)

Under this rule combination SCUs are assumed to develop solely on epicormic shoots, not on lateral axes. Epicormic initiation is limited by the requirement of one inactive lateral axis. Total live shoots at ninety years was plotted against increasing bifurcation for each shoot order, and in general total live shoots show a non-linear increase with increasing parameter values (Figure 4.4). The maximum total live shoots at year ninety is greatest for increases in third order bifurcation and the bifurcation of newly initiated epicormic shoots: 247,911 and 176,054 respectively (Table 4.3). The maximum for increases in first and second order bifurcations are 17,647 and 10,461 respectively. Please note that the relationship between third order bifurcation and total number of live shoots shown is not strictly correct; the model run was halted the next year when total segments exceeded 200,000. The effect of increased average bifurcation for any total live shoots greater than 200,000 likely would be greater in magnitude, and this can be inferred from the year at which the model was stopped due to too many segments. For example, under this rule combination and for an average third order bifurcation of 2.90 the model had 247,911 at year 26. Obviously if it had been possible to run the model to 90 years the total number of live shoots would be exponentially larger.

Slightly different results are obtained with total SCUs at year ninety. There is a vague increase with increasing first order average bifurcation, with total SCUs at year ninety ranging from zero to 125 (Figure 4.5). In contrast, there is a slightly negative relationship between total SCUs and increases in second order bifurcation (Figure 4.5). There appears to be little to no trend with increases in third order average bifurcation, although for higher bifurcations the trend is difficult to analyze due to the early termination of the model if the branch grows too large. This termination often occurred before SCU development began in the simulation, as early as twenty-six years. Within the rules of the model, however, third order bifurcation is not expected to influence the process of SCU formation. The clearest relationship between average bifurcation and SCU development is in the high sensitivity of total SCUs to increases in the average bifurcation of newly initiated epicormic shoots; total SCUs at year ninety ranged from zero to 1021 (Table 4.3; Figure 4.5). These trends can be explained by the relationship between the rules for epicormic initiation and SCU independence. Under this SCU rule, SCUs can only be formed on epicormic axes. In addition, there is a minimum number of shoots that an epicormic complex must have in order to be called a new SCU (10 shoots) and epicormics can only form on first order shoots. Therefore increases in first order bifurcation facilitate the process of SCU formation by increasing the number of first order nodes available for epicormic initiation. Higher first and second order bifurcations also increase the chance that a newly forming SCU produces enough shoots to reach the minimum number necessary for SCU independence. However, SCUs decreased with higher second order bifurcation. This relates to the rule for epicormic initiation; with higher second order bifurcation there is less chance that the subtended lateral shoot is no longer growing; therefore fewer epicormic shoots would be allowed to sprout. The effect of increasing the average bifurcation of newly initiated epicormic shoots on SCU formation is obvious—the probability that a newly forming SCU grows beyond the first two years of epicormic growth is determined by the average bifurcation of newly initiated epicormic shoots. This effect increases both the total number of shoots of the newly forming SCU as well as the first order framework upon which new epicormics can sprout. In the rule structure of the model shoots of order three have no influence on SCU development, other than the number of total shoots on the SCU.

Rule Combination 2 (Table 4.2)

This rule combination 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 year ninety with increasing bifurcation is greater than for rule combination one (Table 4.3). For order one and two bifurcations the maximums of shoots at branch age ninety are 64,442 and 84,096 respectively (Table 4.3; Figure 4.4). The maximum total live shoots for increasing third order bifurcation is 299,206. For the average bifurcation of newly initiated epicormic shoots the maximum total live shoots is 231,999. Since under this rule for there are no restrictions on epicormic initiation, 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 SCU complexes.

With this rule combination the trends for total SCUs with increasing bifurcation are similar to above (Figure 4.5). There is an increase with both first order and initiated epicormic bifurcations, but no relationship with second and third order bifurcations. The magnitude of the effects of increasing first order and new epicormic average bifurcation is greater than for rule combination one. Across all orders the magnitude of the number of SCUs is greater than the number of SCUs formed under the other rule combinations.

Rule Combination 3 (Table 4.2)

In this rule combination epicormic initiation is restricted by the requirement of two inactive lateral axes, and SCUs only form on epicormic axes. The further limitation on epicormic initiation given by this rule is reflected in the maximum of total live shoots at year ninety. The maximum with increasing bifurcation in this case is less than the maximum observed under the first two rule combinations, with the exception of third order average bifurcation (247,210) (Table 4.3; Figure 4.4). An interesting exception here is in second order bifurcation: there is no apparent relationship between increasing second order bifurcation and total live shoots under this rule combination. The major cumulative effect of epicormics in this system is once again clear. With a reduction in epicormic initiation given by this third rule, the effects of all of the other parameters are minimized. The change in the effect of second order bifurcation under this rule combination is most dramatic; it is obviously difficult for both lateral axes to no longer be growing (a requirement for epicormic initiation) with higher second order bifurcations.

The relationship of total SCUs with increasing bifurcation shows a modest increase with increasing first order bifurcation, but a steady decline with increasing second order bifurcation (Figure 4.5). This reflects the further restriction on epicormic initiation set by this rule. The largest increase in total SCUs is seen with increases in the average bifurcation of new epicormic shoots.

Rule Combinations 4-6 (Table 4.2)

Changing the rule for SCU independence so that SCUs can develop on both epicormic and lateral axes has a profound effect on model output. Even at the default parameter values the total live shoots at year ninety is impossibly high, causing a memory error on the computer that occurred under all possible rules for epicormic initiation. 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. For example, when a second order shoot becomes a new SCU, its average bifurcation becomes the same as that of a first order shoot. The third order shoots become second order and so forth. Those new second order shoots can eventually become first order shoots and the process continues. It is clear that this level of sequential reiteration in combination with proleptic reiteration does not occur in *P. menziesii*.

Summary of P. menziesii sensitivity analysis

The increases of third order and new epicormic bifurcations in *P. menziesii* have the greatest effect on total shoots at year ninety across all combinations of SCU and epicormic rules (Figure 4.4). This result is similar to that obtained when the contiguity criterion for SCU independence is used in the simulation model. An increase in the third order bifurcation is similar to assigning it the function of a first order shoot, thereby producing very high orders of shoots. Furthermore, shoots of order greater than three were assigned a reduced bifurcation proportional to the bifurcation of third order shoots. An increase in third order bifurcation is perpetuated through higher orders of branching and it is clear that extensive sequential reiteration would produce very dense trees (as in Borchert and Slade 1984). This significant effect of reiteration is also demonstrated by the impact of increasing the average bifurcation of new epicormic shoots. The non-linear effect of increases in the other parameter values is observed both in the context of reiteration and regular growth under different rule combinations. The restrictions on epicormic sprouting enforced by rule combinations 1 and 3 limit the framework upon which increases in average bifurcations would act by reducing the number of suppressed buds that are released. These restrictions are plausible under the current probability structure because the density of age at epicormic sprout was based on observed epicormics that had *already sprouted*. It did not take into account the suppressed buds that were never released. A restriction such as the ones imposed under both rule combinations 1 and 3 may be a reasonable addition to the probability distribution, which would account for suppressed buds that were never released.

A. grandis sensitivity analysis

Rule Combination 1 (Table 4.2)

With SCU development occurring only on epicormic axes, the implicit assumption under this rule combination is that there is no SCU formation in *A. grandis*; no epicormics are produced in simulations of this species, therefore no new SCUs are created. The maximum of total shoots at year ninety was greatest for increases in order three bifurcation (6456) compared to order one (546) and order two (2786) (Figure 4.6).

In this initial analysis order three bifurcation is only sampled from zero to two. When the upper limit of the sampling range is increased to four, the maximum of total live shoots for order three greatly increases (401,863). For *A. grandis* the reliance on regular shoot growth shows 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, which is seen below to have a profound cumulative effect on branch growth. At the same time, the small effect of increasing first order bifurcation is due to the lower bound imposed on growth—the Poisson process is not used for first order shoots until year fifty, at which time first order bifurcation plays a role in the simulation.

Rule Combination 4 (Table 4.2)

Differences in rules for epicormic initiation were not explored because epicormic initiation was assumed not to have a major impact on the growth of *A. grandis*. The sensitivity analysis of *A. grandis* only compared the two rules for SCU independence. Under this rule, SCUs are allowed to develop on both lateral and epicormic axes and the functional role of the SCU becomes possible in *A. grandis*. Impossibly high shoot totals were produced under this rule combination, again due to the effects of increasing bifurcation with higher orders of shoots. As with *P. menziesii* it is obvious that extensive sequential reiteration in a functional sense is not possible in *A. grandis*. In Chapter III, therefore, units that were observed in *A. grandis* branches that had the characteristics of the SCU were probably not independent, functional structures; in this case the classification of the branches into SCUs was purely an artifact of the structure of branch growth.

Summary of sensitivity analysis for both species

This analysis shows that the effect of increasing bifurcation of higher order shoots of both species has the greatest effect on growth (in terms of total shoots). This effect is more pronounced in the case of *A. grandis*, where growth is dependent upon regular shoots. It is also clear that functional reiteration does not occur in *A. grandis*, whether through proleptic or extensive sequential reiteration. Proleptic reiteration was ruled out in *A. grandis* through the observation of little epicormic shoots growth on the branches of that species. When sequential reiteration is included in the modeling of either species, the branches grow such impossibly high numbers of shoots the model exceeds the memory capacity of the computer. The reordering of lateral axes to function like first order axes does not occur in these species and the observation of SCUs that are not of epicormic origin has no basis in the theory of adaptive reiteration.

Long model runs

P. menziesii

The model was run five times through 400 years, and in general for *P. menziesii* the branches terminated (zero live shoots) around year 300 (Figure 4.7(a)). Plots of total live shoots over time for the five different seed values show fluctuating trends of growth, decline and renewal. Obviously the death of the branch would occur before the total live shoots reaches zero, but this analysis demonstrates that such a mortal decline would eventually occur sometime before year 300. For a population of fifty branches the mean terminal age is 281, and all branches died before year 400 (Table 4.4, Figure 4.8). This indicates that the limitation imposed on SCU growth in the simulation model with increasing epicormic generation is sufficient to result in the observed decline of the entire branch without the inclusion of any external factors. Westing (1964) states that given the infinite growth potential of the meristematic cell line, it is the culmination in height and crown growth that eventually contributes to the death of the tree. Ishii and Ford (2001) found that one way *P. menziesii* overcomes the culmination in crown growth was the process of proleptic reiteration, yet these simulations show that there is a limit to this growth potential. Franklin et al. (1987) describe tree death as a spiral, in which the cumulative effect of events throughout the life of a tree weakens its ability to avoid death with subsequent damaging occurrences. These simulations also show that a tree (or branch) that is grown in isolation will die at some point due to limitations on growth and reiteration of the foliage structure. This is a cautious point, however, because the cumulative effects of the environment are simulated in part through the stochasticity in the model. Such a theoretically isolated tree may not exhibit the same fluctuations in growth that are present in the simulation. These limitations were also imposed in order to observe desired ranges of model outputs, and do not yet have a basis in field observations.

A. grandis

For *A. grandis* it was observed that the eventual loss of the main axis and subsequent reduction in growth with increasing order is sufficient to result in eventual death of the branch. In five different seed runs at default parameter values most branches terminate around year 90 (Figure 4.7(b)). As with *P. menziesii* there are some fluctuations in the trend of total shoots over time, with some decline followed by periods of positive shoot growth. These cycles of renewal, however, are not as common or as pronounced as the cycles observed in *P. menziesii*. For the population of fifty branches the main axis was maintained until the simulation went to the lower crown parameterization, at year fifty. The mean terminal age for this population is 105.94 (Table 4.4; Figure 4.8).

SCU Development in P. menziesii

Plots of total SCUs as well as regular and epicormic shoots per SCU show variable relationships over time. The shape of total number of SCUs over time reflects that observed for total live shoots over time (Figure 4.9), with a peak of 90 SCUs around year 135. Both regular and epicormic shoots per SCU show initial fluctuating patterns over time, then steady relationships (Figure 4.9). This indicates that the average dynamics of SCU growth over time are stable throughout most of the lifespan 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. Table 4.5 gives the total SCUs, total shoots, regular and epicormic shoots per SCU and total miscellaneous shoots on a branch for every ten years through the lifespan of one branch.

The simulation model gives reasonable outputs for the total number of SCUs and the number of shoots per SCU on *P. menziesii* (see Table 3.2 for observed values). In this run an SCU is defined as forming solely on the basis of epicormic shoots, allowing only for proleptic reiteration. It is clear that the purely functional definition of SCU formation through proleptic reiteration may be adequate in the context of the data. Given this, it is of interest to assess the dynamics of SCU formation over time. Demographic plots of total epicormic and regular shoots for a given shoot age were generated every five years for one SCU in the model run (Figure 4.10). The age-class distributions in these plots reflect the distributions described by Ishii and Ford (2001) in the classification of the stages of SCU development. This SCU was declared independent in year 35 (at age 10) and survived through year 60, giving it a lifespan of 35 years. This is reasonable in the context of the data, with the oldest observed SCU 20 years old. It is likely that sometime before year 60 this SCU had so few shoots that were spread out among dead twigs that it would no longer have been classified an SCU in field observations.

The potential lifespan of the SCU with the addition of sequential reiteration can be assessed in the context of the Poisson distribution. The decrease in expected value for the modified Poisson distribution has implications for the number of shoots grown each year, but it 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 on each consecutive year, then the number of years at which the main axis of an SCU is expected to draw its first zero can be modeled by a geometric distribution. The random variable X is the number of years until the main axis draws a zero and the probability of drawing a zero is determined by the Poisson distribution (e^{-Rb}). The probability the main axis is lost on year X and the expected value of X are (Casella and Berger 1990):

$$P(X = x) = p(1 - p)^{x-1}; x = 1,2,...; p = e^{-Rb}$$
$$E(X) = \frac{1}{p} = e^{Rb}$$

For a bifurcation of 2.5, the expected year the main axis is lost is 12.18 ($e^{2.5}$), while for a bifurcation of 3.0 the expected year is 20.09. 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 respectively. 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 ten-eleven years being the maximum foliage longevity). It seems that this probability structure adequately matches the observations of SCU longevity, and further illustrates the importance of the main axis in the *P. menziesii* branching model.

Summary and Conclusions

This model analysis shows that a reduction in growth with increasing complexity of a branching system is sufficient, over time, to result in decline and death of a branch. This occurs regardless of proleptic reiteration, although it is clear that proleptic reiteration greatly increases the lifespan of *P. menziesii*. It has already 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), while in general death of a branch is usually attributable to environmental causes (Westing 1964; Franklin et al. 1987). In this case it may be that regardless of the environmental factors, a branch cannot survive indefinitely given constraints on the complexity of that branch.

Moorby and Wareing (1963) observed that ageing effects in trees may be due to increasing competition for nutrients between shoots as a tree increases in complexity, and that apical dominance effects play an important role in determining the distribution of available nutrients. 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. Competition for nutrients between shoots is dominated thereby by the terminal shoot. Zimmerman (1978) found a distinct hydraulic constriction at branching junctions while Borchert and Honda (1984) observed that hydraulic flux decreased with increasing order, and reductions in bifurcation of higher branching orders is due to the exponential decrease in the flux of lateral branches. Although the current modeling exercise does not address either physiological or physical explanations for limitations on branching complexity, it clearly demonstrates that such limitations are necessary when generating a long-term stochastic model of branch growth. Furthermore, this analysis has demonstrated that through a stochastic modeling process limitations on branch complexity are sufficient to result in eventual death of a branch. It may be that a combination of the processes described above can account for this eventual decline.

Table 4.1: Default bifurcations and seed values used for simulations of branching of *A. grandis and P. menziesii*. Years at which the branch assumes a particular crown position are also given

Species	*P. menziesii*	*A. grandis*
Parameter	Average bifurcation	
1st order	2.5	3
2nd order	1.5	2
3rd order	0.5	1
Initiated epicormic	0.7	NA
Seed		
detailed seed analysis	6,17,28,30,36,47	
seed used for sensitivity	21	29
Crown Position	**Year**	
upper	< 90	<11
middle	(90,150)	(11,50)
lower	>150	>50

Table 4.2: Description of rule combinations used for sensitivity analyses.

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

* Default rule combination

Table 4.3: Summary of results of sensitivity analysis for both species. For *A. grandis* only rule combinations one and four were observed, and changes in new epicormic average bifurcation were not explored.

Rule combination	Species	Parameter	Values sampled	Max. live shoots	Max. SCUs
1	*P. menziesii*	1st order Rb	(0,3)	17,647	125
		2nd order Rb	(0,3)	10,461	80
		3rd order Rb	(0,3)	247,911	92
		new epicormic Rb	(0,3)	176,054	1021
	A. grandis	1st order Rb	(0,4)	546	NA
		2nd order Rb	(0,3)	2768	NA
		3rd order Rb	(0,4)	401,863	NA
2	*P. menziesii*	1st order Rb	(0,3)	64,442	411
		2nd order Rb	(0,3)	84,096	369
		3rd order Rb	(0,3)	299,206	416
		new epicormic Rb	(0,3)	231,999	1228
3	*P. menziesii*	1st order Rb	(0,3)	3287	19
		2nd order Rb	(0,3)	2683	76*
		3rd order Rb	(0,3)	247,210	67**
		new epicormic Rb	(0,3)	107,706	744
4	*P. menziesii*	1st order Rb	(0,3)	NA	NA
		2nd order Rb	(0,3)	NA	NA
		3rd order Rb	(0,3)	NA	NA
		new epicormic Rb	(0,3)	NA	NA
	A. grandis	1st order Rb	(0,4)	NA	NA
		2nd order Rb	(0,3)	NA	NA
		3rd order Rb	(0,4)	NA	NA

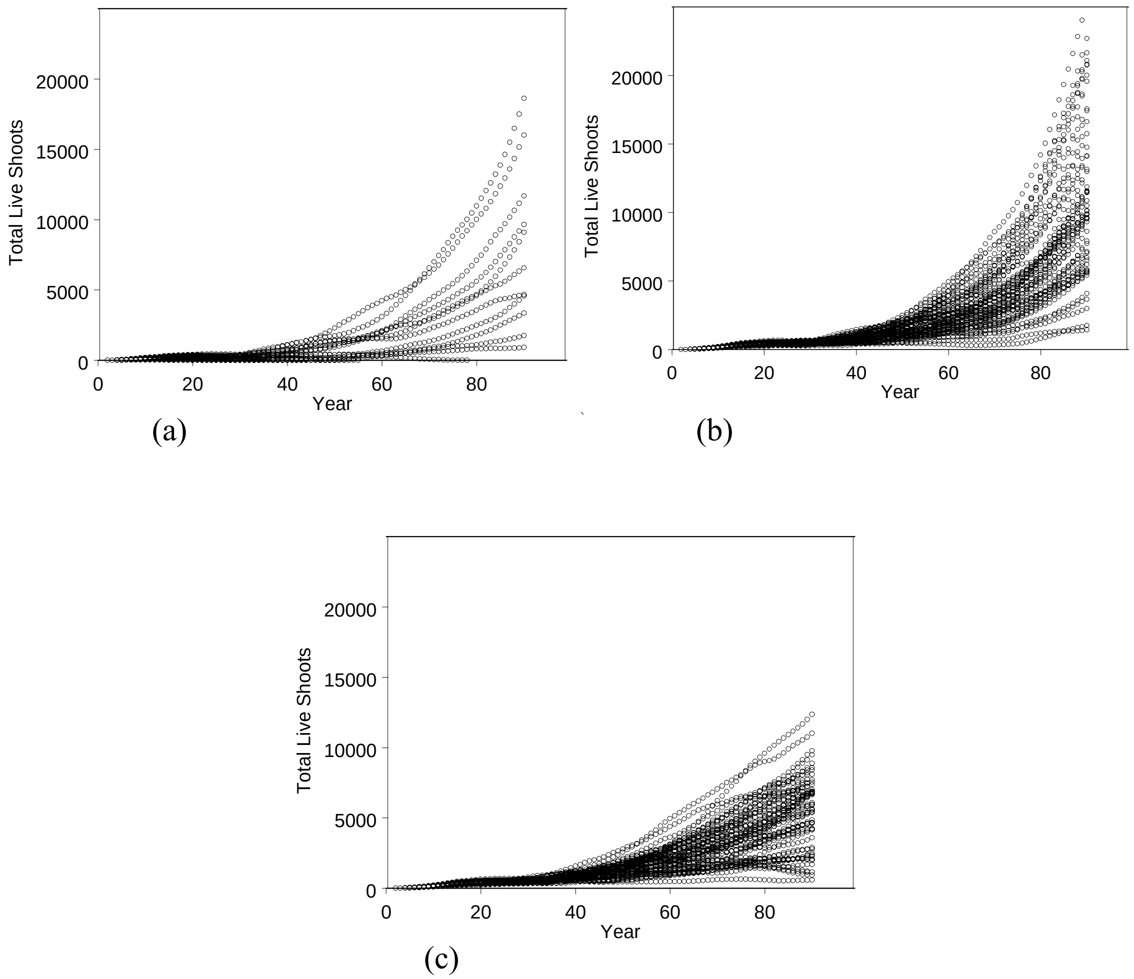
* This maximum was attained for the lowest sampled second order bifurcation.
** This maximum does not reflect an increasing trend.

Table 4.4: Average values for terminal ages of populations of fifty simulated *P. menziesii* and *A. grandis* branches under default parameter values.

Species	*P. menziesii*	*A. grandis*
Main axis	until year 50	until year 50
mean	281	106
median	278	98
standard deviation	56.9	21.84

Table 4.5: SCU dynamics over time for one simulated branch of *P. menziesii* under default parameter values.

Year	Total SCUs	Total shoots on branch	Regular shoots per SCU	Epicormic shoots per SCU
5	1	37	37	0
15	1	271	271	0
25	1	377	374	3
35	1	339	293	46
45	3	517	168	4.33
55	1	785	555	230
65	5	1448	264.8	24.8
75	12	1842	125	28.5
85	22	3426	133.95	21.8
95	35	5096	119	26.6
105	55	7811	120.7	21.3
115	84	11420	116.9	19
125	103	14839	128.5	15.5
135	123	15675	116.6	10.9
145	123	15587	114.9	11.8
155	115	14957	116.7	13.4
165	106	12681	107.8	11.8
175	89	12597	129.8	11.9
185	87	12245	128.2	12.6
195	78	10150	116.6	13.5
205	76	7818	95.8	7
215	52	6644	120.9	6.8
225	41	5182	114.3	12..1
235	35	3593	97	5.7
245	20	2217	104.2	6.7
255	16	1788	100	11.8
265	13	1971	144	7.6
275	11	1156	98.8	6.3
285	7	808	106.6	8.9
295	5	792	152	6.4
305	4	552	127.5	10.5
315	5	541	100.8	7.4
325	4	826	198.8	7.8
335	3	800	258	8.7
345	3	409	132	4.3
355	1	59	55	4



(a)

(b)

(c)

Figure 4.1: Plots of total live shoots over time for *P. menziesii.* (a) original model with 50 runs at the same parameter values. (b) Fifty runs with the addition of a lower bound in the growth of the regular main axis. (c) Fifty runs with the addition of an upper bound on growth.

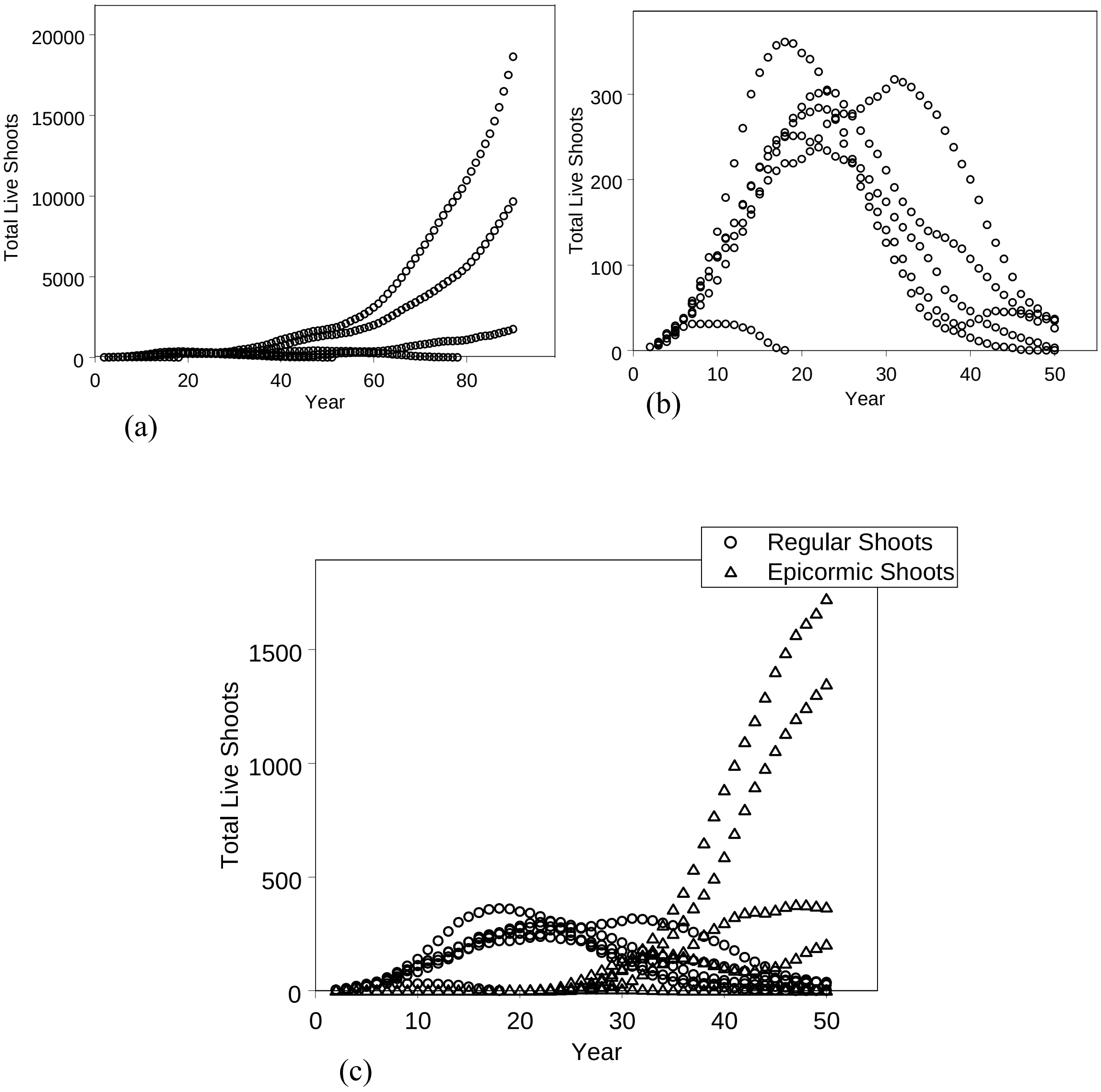


Figure 4.2: Plots of total shoots over time up to year ninety for *P. menziesii* with no bounds on growth
(a) There are highly variable results at the six seed values. (b) A plot of regular shoots over time up to year 40 implies almost identical growth patterns. (c) Divergence occurs in the pattern of epicormic shoots, which is obvious as early as year 40.

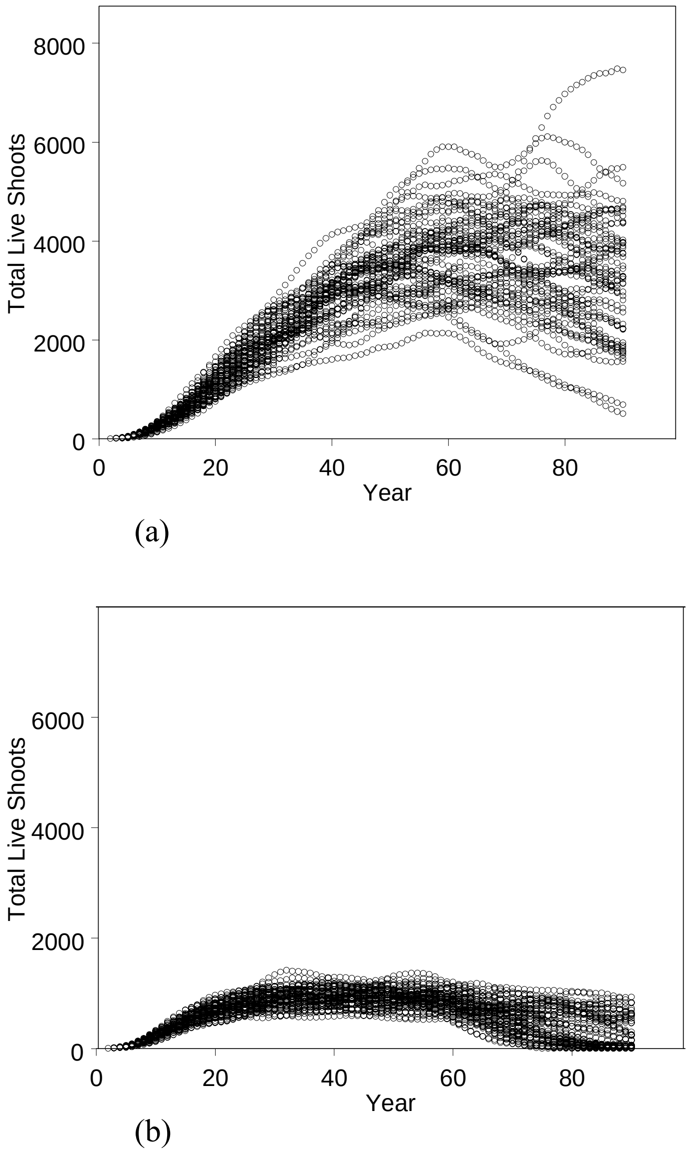
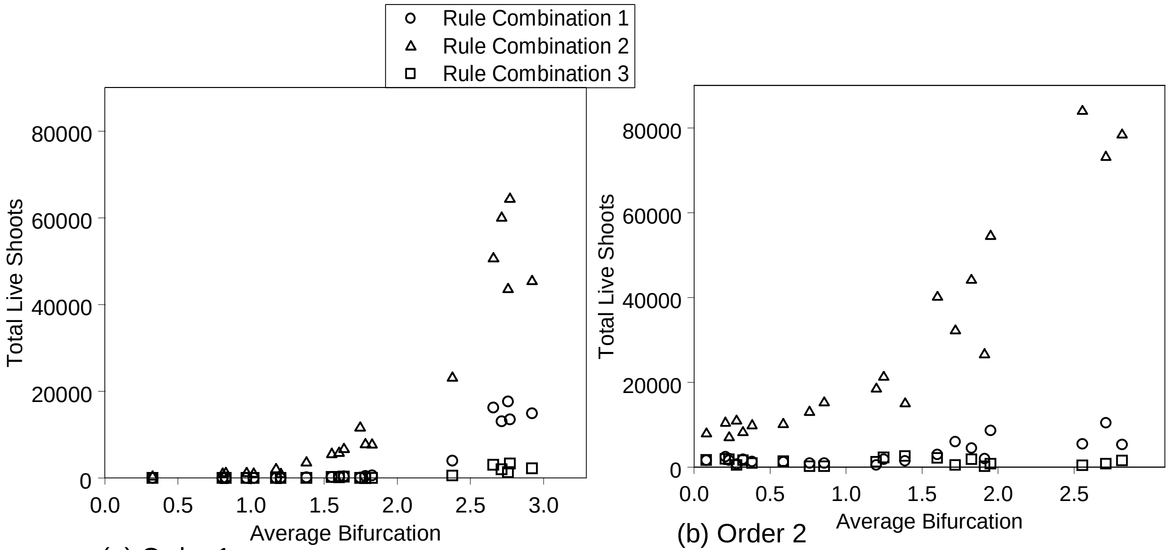


Figure 4.3: Plots of total live shoots over time for *A. grandis*.

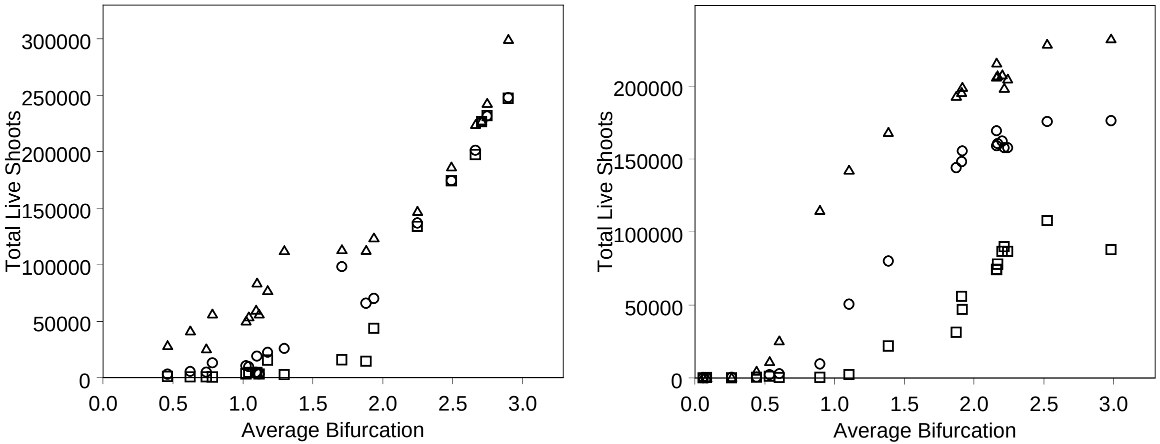
(a) There is unrealistically high variability in the original model with fifty runs at the same parameter values.

(b) When a reduction in bifurcation with increasing order greater than three is imposed in the model, the range is greatly reduced.



(a) Order 1

(b) Order 2

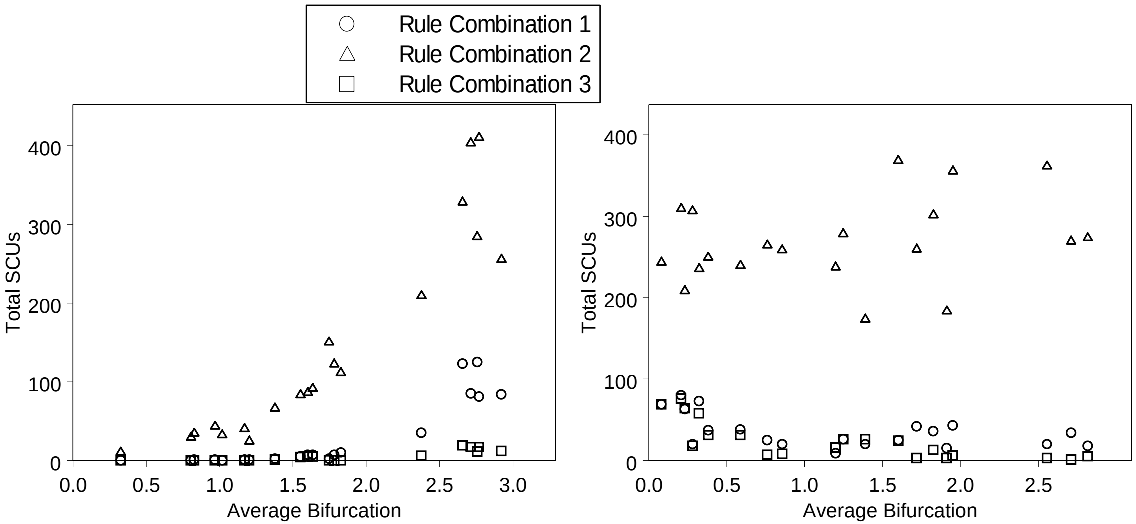


(c) Order 3

(d) New
Epicormic

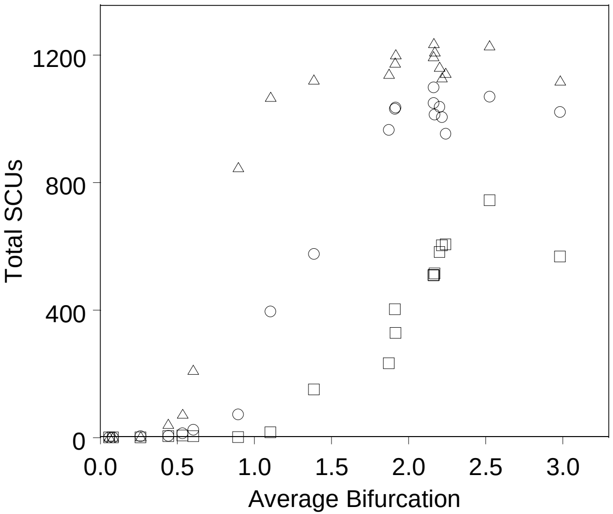
Figure 4.4: Live shoots at year 90 of *P. menziesii* with increasing average bifurcation at three different rule combinations.

Response to increases in (a) first order; (b) second order; (c) third order; (d) new epicormic shoots. Note the different scale for live shoots of third order and new epicormic shoots.



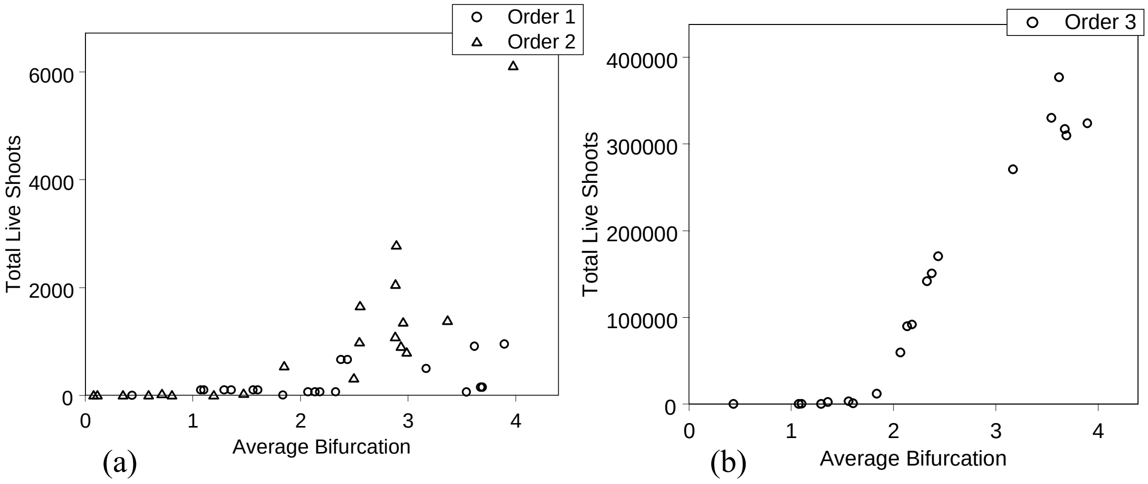
(a) Order 1

(b) Order 2



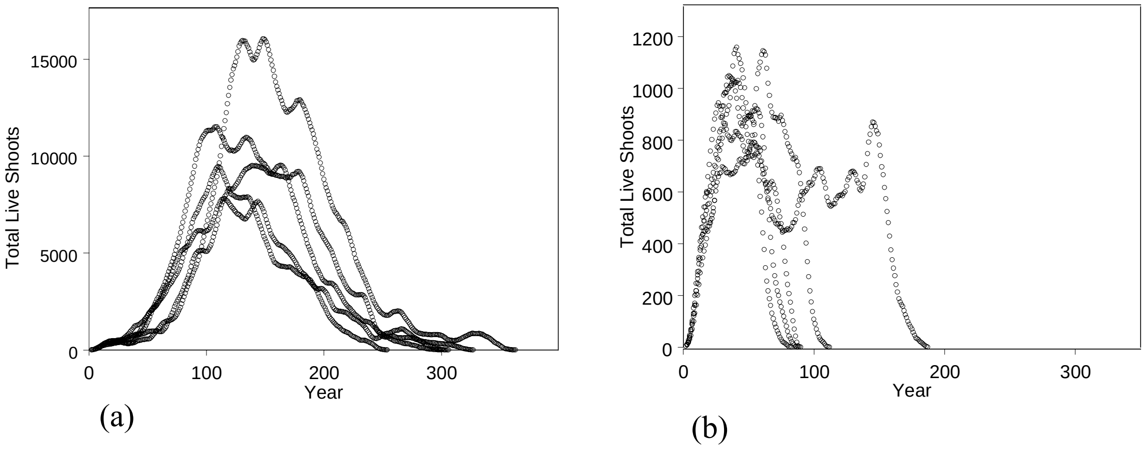
(c) New
Epicormic

Figure 4.5: Total SCUs at year 90 of *P. menziesii* with increasing average bifurcation at three different rule combinations.
Response to changes in (a) first order; (b) second order (c) new epicormic shoots. Note the different scale for total SCUs of new epicormic shoots. Order three is excluded because there is no relationship between third order shoots and SCU development.



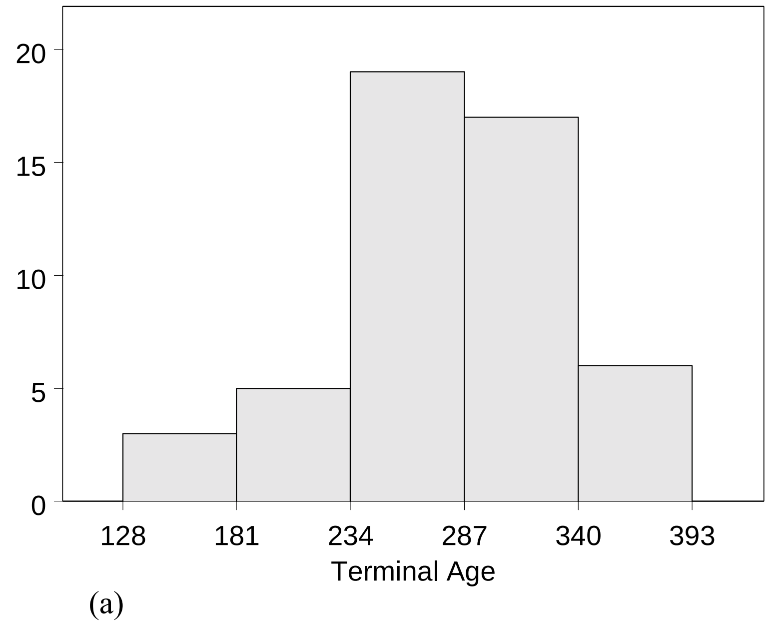
(a) (b)

Figure 4.6: Total live shoots at year 90 in *A. grandis* with increasing bifurcations under rule combination 1. Response to changes in (a) first and second order; (b) third order.



(a) (b)

Figure 4.7: Total live shoots over branch lifespan for (a) *P. menziesii* and (b) *A. grandis* at default parameter values. Please note the different axis scale for (b).



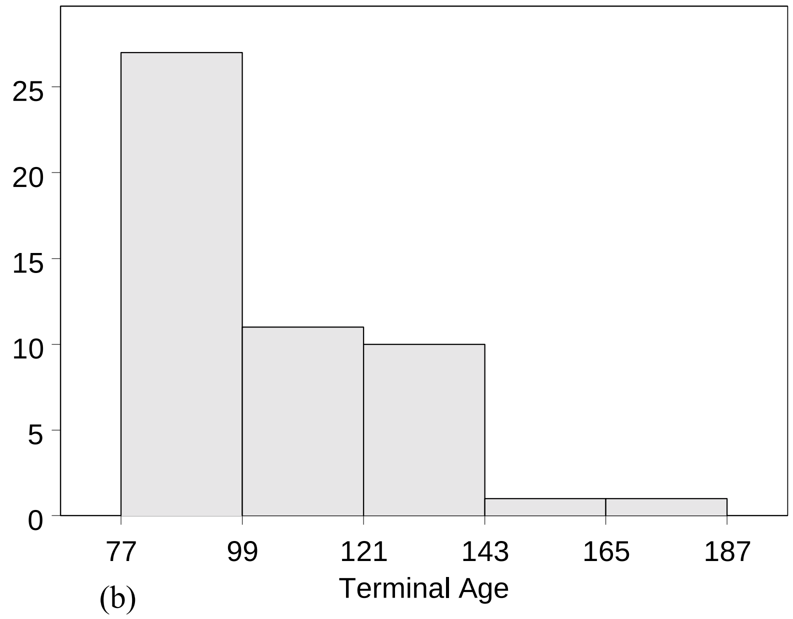


Figure 4.8: Frequency histograms of the terminal ages of populations of fifty branches of (a) *P. menziesii* and (b) *A. grandis* under default parameter values.

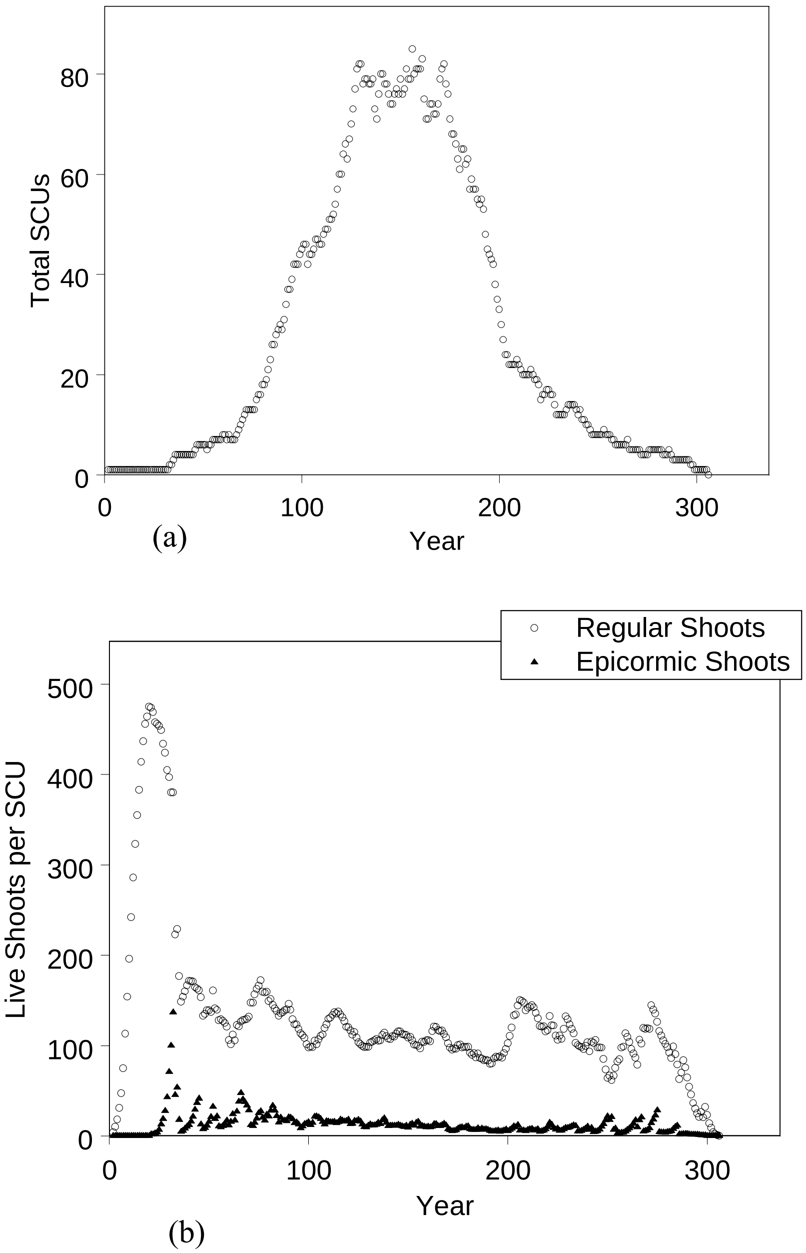
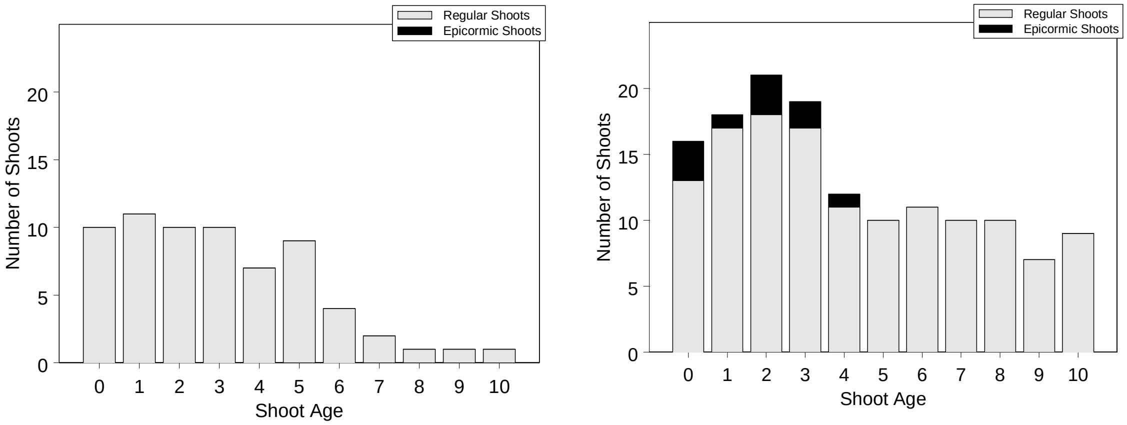
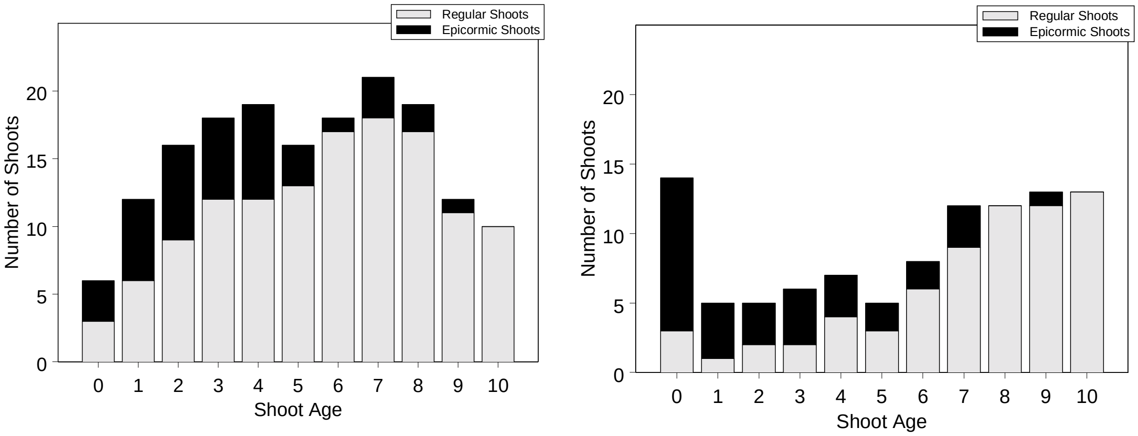


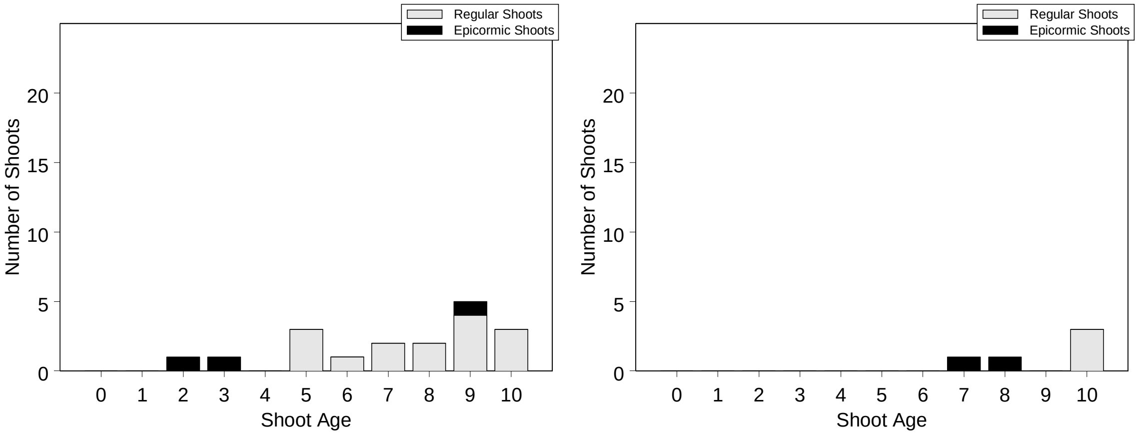
Figure 4.9: Scatter plots of SCU dynamics for a single branch in *P. menziesii* under rule combination 1. A plot of SCUs over time shows a shape similar to total live shoots (a), while regular and epicormic (b) shoots per SCU show more steady relationships with time.



Year 35 Year 40



Year 45 Year 50



Year 55 Year 60

Figure 4.10: Plots of SCU shoot demography for an SCU through years 35-60. The plots were generated every five years. The plots exhibit some of the stages of SCU development outlined by Ishii and Ford (2001).

Chapter V

Summary and Conclusions

General contrast of growth in *A. grandis* and *P. menziesii*

The data gathered in this study have provided insight into the crown processes of old-growth *P. menziesii* and *A. grandis* trees (Chapter I, Chapter III). In *P. menziesii* it was confirmed that proleptic reiteration plays a vital role in foliage regeneration (Chapter III) and that *A. grandis* branches rely on strong apical dominance, growth of the terminal meristem, and higher bifurcation on higher orders of branching (Chapter III, Chapter IV). On the foliage level *A. grandis* needles hold more weight per unit area than *P. menziesii* (Figure 3.5) and needles on *A. grandis* shoots fall off sooner than needles on *P. menziesii*. Overall *P. menziesii* branches are longer and have greater foliage area and mass than *A. grandis* branches, but without epicormics the foliage mass and area on *A. grandis* branches exceeds *P. menziesii* (Figure 3.4). These results begin the important process of contrasting the growth properties of these two species, yet the degree of inference possible is narrowed by the limitations on sampling and stringent experimental design in old-growth forests. The flexibility of computer simulation models allows for the detailed observation of the development of old-growth branches given the descriptive data obtained in the field study of *A. grandis* and *P. menziesii*.

Reiteration in *A. grandis* and *P. menziesii*

The importance of reiteration in the growth of trees has previously been observed by Halle et al. (1978) in tropical forests and in a few temperate species (Begin and Filion 1999). Ishii and Ford (2001) claimed reiteration of the SCU allowed foliage regeneration and contributed to the survival of old *P. menziesii* branches. This proleptic reiteration is especially important when crown expansion has ceased and terminal growth is minimal (Ishii and Ford 2001). Field observations of this reiteration made quantitative definitions of the SCU difficult to universally apply (Chapter II). In the destructive sampling of *A. grandis* it was decided to use the most general and descriptive definition, i.e. a cluster of shoots with a distinct main axis and 2-3 lateral shoots per year, spatially separated from other such clusters via foliage death (Chapter III). This sampling procedure allowed for comparisons between *A. grandis* and *P. menziesii*, but subsequent modeling exercises revealed no functional unit such as the SCU in the growth of *A. grandis* branches (Chapter IV). It is clear that reiteration contributes significantly to the growth of *P. menziesii*, explaining how Ishii and Ford (2001) observed branches up to 155 years old, while in *A. grandis* there was no contribution of reiteration to growth. The oldest observed branch of *A. grandis* was only 63 years old (Table 3.2).

The dominating effect of reiteration on branch growth became evident through stochastic computer simulations of both *A. grandis* and *P. menziesii* (Chapter IV). Proleptic reiteration created significant cumulative effects on populations of *P.* menziesii branches generated with the same parameter values, even when upper bounds were created for the proliferation of reiterative complexes (Chapter IV). Similar upper bounds were required for the proliferation of higher orders of branching, indicating limitations on branch complexity regardless of the form of growth (proleptic or sequential). Branches produced with these limitations still showed an exponential increase in growth with increasing branch age, but longer model runs revealed a peak in that growth with a subsequent decline and eventual death of the branches (Figure 4.6).

This important result rests on a few theoretical assumptions that do not yet have a basis in empirical observation. For example, the need for some form of decline is obvious from the model results and I proposed a continuous reduction in growth with increasing generation for new epicormic shoots; from such a reduction it immediately follows that the branch would eventually cease to produce new shoots. In the model simulation the probability of drawing a zero becomes higher as the bifurcation ratio decreases, such that eventually there are no shoots that can sprout epicormics to renew the cycle of reiteration. Although the assumption of continuous decline is purely speculative, I believe further analysis would show that other forms of growth decline would still result in death of branches with increases in complexity, i.e. increases in the number of lateral junctions (whether formed through sequential or proleptic growth). This reduction could occur on a different temporal scale. Death of an individual SCU complex is inevitable, so once the potential for reiteration is reduced the mechanism by which individual SCU complexes are generated is lost. Whether this occurs at 150 years or 600 years would depend on the form of growth reduction that is chosen.

Although it is clear that proleptic reiteration does occur in *P. menziesii* and not in *A. grandis*, it is still possible that a limited form of traumatic sequential reiteration occurs on these branches; with the loss of the terminal bud lateral shoots assume the role of the main axis within the usual sequential timing of growth (Figure 1.1). This has been observed in the vertical growth of the terminal bud in various species (e.g. Harding 1986) and could serve as a more realistic form of a lower bound on branch growth wherein the horizontal branch main axis is maintained through sequential reiteration. This would be expected to increase the lifespan of *A. grandis*, although limitations on complexity would need to be imposed in this case as well. These limitations are indicated by the enormous impact ubiquitous sylleptic reiteration was shown to have on branch growth (Chapter IV, Figure 4.5(c)). Such sequential reiteration would be maintained as a feature of the main axis of the SCUs throughout the branching structure, and would create a separate basis for the formation of new SCUs.

The establishment of sequential reiteration in the model would create a few interesting problems. How does one quantify the rules under which a lateral shoot assumes the role of the apical meristem? What if the lateral shoot is no longer active—would it be appropriate to release a suppressed bud on a higher order shoot? How can this type of reiteration be ordered in a functionally specific manner? The resolution of these issues will be possible only through further analysis and observation of this system.

Although simulations have revealed some issues in a functional definition of the SCU (Chapter IV), the stages of SCU development outlined by Ishii and Ford (2001) have been qualitatively mirrored in model outputs (Figure 4.9). The visual definition of the SCU, in which an SCU is recognized through its architectural characteristics and not from its course of development (e.g. any cluster of shoots that have those characteristics, regardless of their origin or relationship to the rest of the branching structure), must be further refined. Under the visual characterization most temperate coniferous species with determinate growth could technically be divided into SCUs. Rather than relating to an important functional unit however, these SCUs would more likely be structural units, as was demonstrated to be the case in *A. grandis* (Chapter IV). I propose the classification of SCUs into their various functional or structural origins as a first step to a more analytical approach in the study of reiteration in *P. menziesii* and the application of this theory to other temperate coniferous species. In this context I believe SCUs can be classified functionally as proleptic (on the basis of epicormic sprouting) or sequential (on the basis of sequential growth and in response to the loss of the apical meristem), or non-functionally as simply structural units. Study of the branching systems under such classifications can be a step in incorporating the different modes of reiteration into the geometric simulation model.

The utility of the contrast

The study of both *P. menziesii* and *A. grandis* trees has proved a useful context for advancing knowledge of branch growth in old trees. Analysis of these superficially similar trees magnified the underlying differences in their growth patterns. The simulation of *A. grandis* branches without epicormic sprouting showed how significant epicormic growth and reiteration are for *P. menziesii*. Field data gathered for both species facilitated model development and subsequent assessment, and led to a key finding in model analysis; limitations on complexity are absolutely necessary in a long-term model of branch growth.

The role of computer simulations in the understanding of branch growth

Geometric simulations of tree and branch form have been studied for thirty years, and have addressed various issues in tree growth (Chapter I). A simulation model that incorporates reiteration into a stochastic branching model over long periods of branch growth has particular complications, and much has been learned from attempts to overcome those complications (Chapter II, Chapter IV). This modeling exercise shows that the incorporation of reiteration into a long-term stochastic model of growth can reveal important processes that are impossible to fully observe in the field. However, the further issues model analysis has raised (such as the need for both sequential and proleptic reiteration) illustrate that modeling cannot be fully representative of the system at hand; however, it is as much the deficiencies of a model as the successes that have heuristic value. Continued study and analysis will only enhance the learning potential of the model. Two modifications of the simulation model have already been proposed above: the inclusion of sequential reiteration in the branching structure and a refinement of the process of growth reduction with increasing generation.

Further Research

This study represents an important step in the understanding of the growth and development of branch form in old trees. Some modifications to the simulation model will be necessary to explore the idea of two potential forms of reiteration in temperate coniferous trees and the consequences of these forms of reiteration for long-term growth. A more detailed assessment of the simulation model will be an important step in accomplishing further progress in understanding of these branching systems.

The predictive value of the constants used in the model can be assessed by comparing the area and weight of the branches in the model to data values. Another sensitivity analysis can also be performed to assess the model for uncertainty in the predicted constants—SNA, foliage weight per shoot length, length ratio of higher ordered shoots, and branching angle. Changes in branching angle and length ratios would be expected to result in changes in branch shape (width and length) that can be compared to field observations. Changes in foliage weight per shoot length would impact foliage longevity and the age distribution of shoots on the branch, while SNA would obviously impact the distribution of foliage area on the branch.

In addition, the use of an optimization procedure would be instructive in exploring ranges of bifurcation ratios that can result in desired simulation outputs. Particular issues would arise in such a procedure due to the high variability over time that has been observed in model runs with the same parameter values, even with the addition of model bounds (Chapter IV). A further complication results from the modification of the Poisson distribution used in the model; the bifurcations would need to be assessed in the context of the decreased expected value of the modified distribution. Also, a better quantification of reduced epicormic growth with increasing generation should also be explored.

An implicit assumption throughout this study has been that the aspects of growth observed for *P. menziesii* are particular to old trees and represent a distinct phase in the life-span of *P. menziesii*. While young *P. menziesii* trees have been extensively studied, none have been observed in the context of these new discoveries in the old, large trees. It would be prudent to analyze branching in young *P. menziesii* with reference to the role (if any) of both sequential and proleptic reiteration, using both field observations and further modifications to the simulation model. It will be of interest to see what changes are necessary in the simulation to successfully model young trees. These observations will have potential implications in the management of young *P. menziesii* forests to old-growth conditions.

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Appendix A
Random number generation for the gamma distribution

The relationship between the gamma and exponential distributions is utilized in random number generation. If you have a random variable X_i that is distributed as an exponential(β), then:

$$f_{x_i}(x_i) = \frac{1}{\beta} e^{-\frac{x_i}{\beta}}$$

$$Y = \sum_{i=1}^{\alpha} X_i \sim gamma(\alpha, \beta)$$

Also, for any probability distribution f_x, if $Z=F_x$ is defined as the cumulative density function of f_x:

$$F_x(x) = \int_{-\infty}^{x} f_x(x) dx$$

$$Z = F_{X_i}(x_i) = \int_0^{x_i} \frac{1}{\beta} e^{-\frac{x_i}{\beta}} dx_i = 1 - e^{-\frac{x_i}{\beta}}$$

then Z~uniform(0,1) (Casella and Berger 1990). Therefore random numbers generated from a uniform distribution can be transformed to an exponential random number. One can then generate a gamma random number by drawing a desired number of exponential variables and summing them. Algorithms for random number generation were taken from Press et al. (1992).

Appendix B
Maximum height of *A. grandis*

The maximum height of *A. grandis* trees at the WRCCRF was calculated using the exponential generalization of the following allometric equation (Ishii et al. 2000; Thomas 1996):

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

where the model is tree height predicted by tree diameter with three estimated parameters: a, b and maximum height ($H_{max,}$ Figure B.1). A plot of height against diameter (Figure B.1) shows an asymptotically increasing function, with the maximum height assumed to be the asymptote. Utilizing the non-linear least squares (nls) function in S-Plus the following equation was generated (Table B.1):

$$H = 50.992*(1-\exp(-0.0006*D^{2.003}))$$

with the predicted maximum height 50.992 ~ 51.0 m.

Table B.1: Parameter estimates and associated standard errors in the asymptotic height relationship of *A. grandis*.

Parameter	Estimate	Standard Error
H_{max}	50.99	3.02
a	-0.00063	0.00067
b	2.003	0.3068
Residuals	NA	4.6917

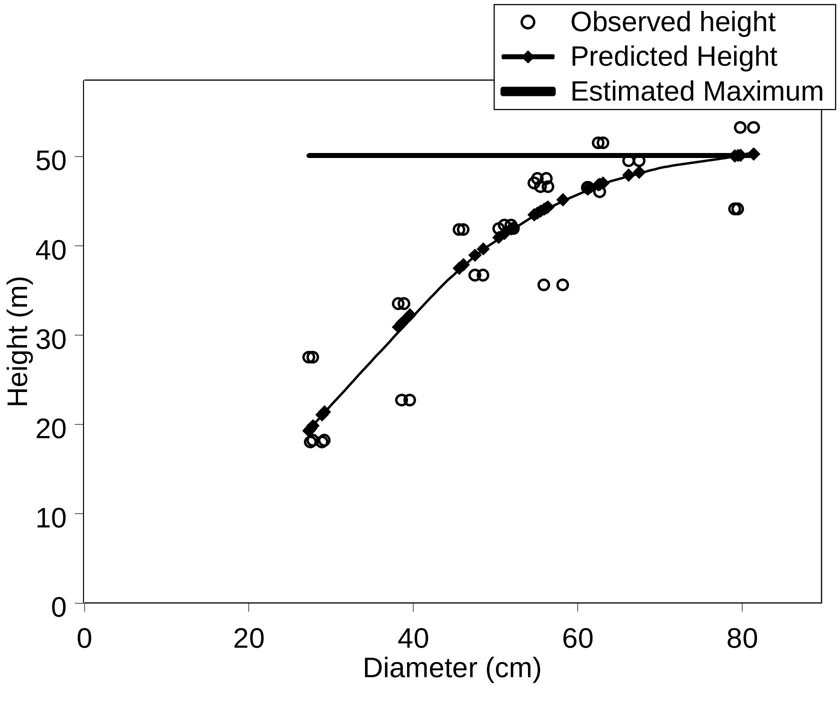

Figure B.1: Asymptotic relationship between height and diameter of *A. grandis*.

Appendix C
Detailed tables of analyses presented in Chapter III

Table C.1: General form of regression analyses, including all transformations used. Y is the response variable and X_i is the individual predictor variable. A (+) indicates a main effect while (*) indicates an interaction effect. β_i is an estimated parameter, where β_0 is the intercept value. Q_i is dummy variable coding for categorical predictors. Examples given are for two response variables.

Regression Type:	Regression equation
Multiple Linear	$Y = \beta_0 + \beta_1 * X_1 + \beta_2 * X_2 + \beta_3 * X_1 * X_2$
Log transformation of Y	$\ln(Y) = \beta_0 + \beta_1 * X_1 + \beta_2 * X_2 + \beta_3 * X_1 * X_2$
	$Y = \exp(\beta_0 + \beta_1 * X_1 + \beta_2 * X_2 + \beta_3 * X_1 * X_2)$
Square root transformation of Y	$\sqrt{Y} = \beta_0 + \beta_1 * X_1 + \beta_2 * X_2 + \beta_3 * X_1 * X_2$ $Y = (\beta_0 + \beta_1 * X_1 + \beta_2 * X_2 + \beta_3 * X_1 * X_2)^2$
Piecewise linear regression: BP=breaking point	$Y_i = \beta_0 + \beta_1 x X_{i1} + \beta_2(X_{i1} - BP)X_{i2}$ $X_{i2} = 1$ if $X_{i1} > BP$, 0 otherwise
Linear with dummy variables Example given with 3 crown positions	$Y_i = \beta_0 + \beta_1 * X_1 + \beta_2 * Q_1 + \beta_3 * Q_2$
	Upper crown: $Q_1=Q_2 = 0$; $Y_i = \beta_0 + \beta_1 * X$
	Middle crown: $Q_1= 1$, $Q_2= 0$; $Y_i = (\beta_0 + \beta_2) + \beta_1 * X$
	Lower crown: $Q_1= 0$, $Q_2 = 1$; $Y_i = (\beta_0 + \beta_3) + \beta_1 * X$

Table C.2: Regression values for foliage width as predicted by length in *A. grandis*. t-tests were performed on two null hypotheses: slope is equal to zero (apriori) and slope is equal to one (priori). Significant slopes are in bold. No intercepts were significantly different from zero.

crown position	parameter	Value	t-value H_0:slope= 0	p-value	t-value H_0:slope= 1	p-value
upper	intercept	-4.2732	-0.5172	0.6235	NA	NA
	slope	1.0431	5.5799	**0.0014**	0.231	0.82
middle	intercept	9.4622	6.5324	<0.001	NA	NA
	slope	0.6561	11.5409	**<0.001**	-6.61	<0.001
lower	intercept	-0.5077	-0.1374	0.892	NA	NA
	slope	0.9286	9.3865	**<0.001**	-0.7219	0.474

Table C.3: Regression lines for foliage length as a function of width in *A. grandis* with the non-significant intercepts omitted. t-tests were performed twice, with H_0 $\beta=0$ and H_0 $\beta=1$. Standard error decreased and fits were improved by setting the intercept to zero.

crown position	slope	standard error	t-value $H_0:\beta=0$	p-value	R^2	t-value $H_0:\beta=1$	p-value
upper	0.9532	0.06481	14.7	< **0.001**	0.97	0.722	0.496
middle	NA						
lower	0.9157	0.0307	29.79	< **0.001**	0.96	-2.75	0.008

Table C.4: ANOVA table for foliage length as predicted by SCU age and SCU position, separated by crown level in *A. grandis*. At all crown levels both are significant either as main effects or in their interaction.

Crown Level		F value	MSE	p-value
upper	SCU position	11.48	921.48	**0.027**
	SCU age	10.58	849.57	**0.031**
	interaction	0.085	6.771	0.78
middle	SCU position	3.22	175.92	**0.077**
	SCU age	74.24	4052.3	<**0.001**
	interaction	47.87	2612.9	<**0.001**
lower	SCU position	29.83	2005.57	<**0.001**
	SCU age	8.57	576.53	**0.006**
	interaction	5.75	386.87	**0.022**

Table C.5: Regression lines for foliage length with SCU age as the predictor in *A.grandis*. All lines show a significant positive slope, indicating an increase of foliage length with the age of the SCU.

Crown Position		Value	t-value	p-value
upper	intercept	-1.69	-0.200	0.85
	slope	6.59	5.35	**0.0017**
middle	intercept	11.91	6.35	**<0.001**
	slope	1.86	6.84	**<0.001**
lower	intercept	23.64	9.58	**<0.001**
	slope	0.878	5.82	**<0.001**

Table C.6: ANOVA table for the SNA of all *A. grandis* branches, showing the main effects of age, SCU position, crown position and their two-way interactions. Analysis of the combined crown positions required a log transformation of SNA to stabilize the variance.

Variable	Mean Squared Error	F value	p-value
age	9.09	204.1	< **0.001**
SCU position	0.74	16.58	< **0.001**
crown position	2.96	66.46	< **0.001**
age* SCU position	0.24	5.42	**0.02**
age*crown position	1.4	31.51	< **0.001**
SCU position * crown position	0.22	5.09	**0.006**
3-way interaction	0.25	5.72	**0.003**
residuals	0.04		

Table C.7: Comparison of the SNA of *P. menziesii* with *A. grandis* across shoot age at three crown positions. The ANOVA was performed without the current year shoots for *A. grandis*. There is a significant difference between the two tree species.

Variable	Mean Squared Error	F value	p-value
shoot age	261599.2	7597.113	< **0.001**
crown position	176972.3	5139.46	< **0.001**
species	69826.5	2027.834	< **0.001**
shoot age * crown position	4870.2	141.435	< **0.001**
shoot age * species	1727.6	50.171	< **0.001**
crown position * species	1293.8	37.573	< **0.001**
shoot age * crown position * species	563.2	16.355	< **0.001**
Residuals	34.4		

Table C.8: ANOVA of foliage mass per shoot length comparison of *A. grandis* and *P. menziesii*. When all crown positions are considered together, tree species is non-significant as a main effect, but significant in interactions.

Variable	Mean Squared Error	F-value	p-value
species	< 0.001	0.022	0.88
crown position	0.351	789.80	< **0.001**
shoot age	0.367	826.39	< **0.001**
species*crown position	0.026	58.72	< **0.001**
species*shoot age	0.0035	7.93	**0.004**
shoot age*crown position	0.0035	7.83	< **0.001**
residuals	0.00044		

Table C.9: *A. grandis* length ratio. The response variable was log transformed to stabilize the variance.

Variable	df	MSE	F value	p value
parent order	1	1.65	19.72	**< 0.001**
crown position	2	0.14	1.64	0.20
angle	1	0.076	0.91	0.34
angle*crown position	2	0.23	2.75	**0.065**
Residuals	349	0.08		

Table C.10: Comparison of the length ratios of *A. grandis* and *P. menziesii* (ANOVA). No transformation was necessary.

Variable	df	MSE	F value	p value
parent order	1	0.67	33.66	**< 0.001**
Crown position	2	0.23	4.57	**0.010**
species	1	0.21	4.28	0.39
parent order*crown position	2	0.13	2.7	**0.068**
parent order*species	1	< 0.001	< 0.001	0.98
crown position*species	2	0.16	3.31	**0.037**
3-way interaction	2	0.14	2.76	**0.064**
Residuals	661	0.50		

Table C.11: *A. grandis* branching angle ANOVA. Crown position is significant in interactions

Variable	DF	MSE	F value	p value
parent order	1	213.06	3.97	**0.047**
crown position	2	120.9	2.25	0.107
parent length	1	24.4	0.47	0.492
parent order*crown position	2	211.0	3.93	**0.020**
parent length*crown position	2	169.0	3.15	**0.044**
Residuals	356	53.8		

Appendix D
Code for the geometric branching model, written in the C programming language using Microsoft Visual C++

Code for all model functions

```
#include <stdio.h>
#include <math.h>
#include <stdlib.h>
#include <string.h>
#include <malloc.h>
#include <time.h>

#include "mod1.h"
#include "ran.h"
// header file with structure definitions and function declarations

int rb, n, nbr, nseg,
segNum,startyr,endyr,nepis,nebr,scuNum,ag,nsbr,nesbr,gn,ord;
// global variables for model--used in almost every function

int param,rule,eprule,alpha;
double rb_a,rb_b,rb_c,rbepi_a,rbepi_b,beta,yr;
//parameters to be read in

long seed;
long ranseed;

double br_length,dout;
int pretip,posttip;
//count of live tips each year

int branch,mort_flag;
//flag of branch mortality--run model while branch==1

int pop;
// for POMAC--keeps track of which vector population on, names output
accordingly

int spp, crown;
//flag from user, indicates whether PSME (spp=1) or ABGR (spp=2) and crown
position (1=upper, 3=lower)
//parameterization to be used

time_t t;
// to seed the random number generator in run_setup


char epinioutfilname[21],sgsoutfilname[21],epioutfilname[21];
char
epiinfilname[21],sgsinfilname[21],sgsinfile[21],epinfile[21],scuin[21],scuout[2
1],epiout[21],sgsout[21];
char
sgsplot[21],iniplot[21],epiplot[21],mortplot[21],epimortplot[21],inimortplot[21
];
char argfile[21],params[21],scunum[21];
// declaration of character strings that store output filenames

typedef struct segs SEG, *SEGPTR;
```

```
SEGPTR *shoot;

typedef struct scu SCUS, *SCUPTR;
SCUPTR *num_scu;
// pointers for the three data structures

int numScu;
int SCUNum[400000];

void main()
{
  rule=0;
  eprule=0;
// Declares the rule combination under which the model is working

  FILE *fgam;
  fgam=fopen("c:\\gammaout.txt","w");
  fprintf(fgam,"age.sprt\tyear\n");
  fclose(fgam);

  FILE *fran;
  fran=fopen("c:\\rannum.txt","w");
  fprintf(fran,"year\tran.num\n");
  fclose(fran);


  FILE *fpois;
  fpois=fopen("c:\\poisout.txt","w");
  fprintf(fpois,"sons\tyear\n");
  fclose(fpois);


  FILE *rbp;
  rbp=fopen("c:\\rb.txt","w");
  fprintf(rbp,"Pop\tYear\tpretips\tposttips\tparam\n");
  fclose(rbp);
// The "rb.txt" file is to keep track of the bifurcation ratios each year the
model is run

  FILE *fpdor;
  fpdor=fopen("c:\\dormant.txt","w");
  fprintf(fpdor,"Pop\tYear\tdormant.buds\tParam\n");
  fclose(fpdor);
// The "dormant.txt" file is to keep track of the number of dormant buds formed
  each year

  FILE *fplive;
  fplive=fopen("c:\\liveshoots.txt","w");
  fprintf(fplive,"Pop\tYear\ttot.shoots\tbrepishoots\tscuepishoots\ttotalsegs
                                                       \tnumSCU\tmain_axis\n");
  fclose(fplive);
// The "liveshoots.txt" file is to keep track of total live shoots each year
      (vs. new shoots kept track of in "rb.txt"

  spp=1;

// Function to create a random sample of parameter values for sensitivity
  analysis, will be taken care of by POMAC

  FILE *fpscu;
```

```
  fpscu=fopen("c:\\numscu.txt","w");
  fprintf(fpscu,"pop\tyear\tshoot_age\tgen\tscuNum\tshoot.cnt\tepi.cnt\n");
  fclose(fpscu);
// The "numscu.txt" file tracks the number of SCUs each year

/* FILE *fpcom;
  fpcom=fopen("c:\\seedcompare.txt","w");
  fprintf(fpcom,"pop\tyear\tage\torder\tn.shoots\n");
  fclose(fpcom);

  FILE *comptwo;
  comptwo=fopen("c:\\seedcomparetwo.txt","w");
  fprintf(comptwo,"pop\tyear\torder\tage\tn.shoots\n");
  fclose(comptwo);
*/
// The files above were used for detailed comparison of seed values
  FILE *fout;
  fout=fopen("c:\\pareto\\critout.txt","w");
  fprintf(fout,"pop\tyear\tshoots\tarea\tweight\tnumScu\n");
  fclose(fout);

  param_sample(); // for sensitivity analysis only!
  int i;
  pop=0;
  for(i=1;i<2;i++)
  {

   FILE *fpar;
   char fileLine[81];
   fpar=fopen("c:\\pareto\\paretoin.txt","r");
   fgets(fileLine,84,fpar);
  // This initializes the file from which the parameter values will be read in


  // srand(time(&t));
  // seed=-time(&t);
  // printf("%f\n",seed);


   while (!feof(fpar))
// this runs the model for each line in the parameter file
   {
//     ranseed=-i;
    ranseed=-5;
    mort_flag=0;
    branch=1;
   // The branch flag is one as long as the model is running, before the branch
dies or the max year

    n=1;

    pop+=1;
    run_setup(); //re-seeds the random number for each population
   // pop keeps track of the parameter set

    fscanf(fpar,"%lf %lf %lf %lf %lf %lf\n",
                                  &rb_a,&rb_b,&rb_c,&rbepi_a,&rbepi_b,&yr);
   // scan in the current line in the parameter file

    alpha=8;
```

```
    beta=0.7;
    printf("%lf %lf %lf %d %lf %lf %lf\n",
                                    rb_a,rb_b,rb_c,alpha,beta,rbepi_a,rbepi_b);

    printf("Beginning population %d\n",pop);
    //printf("%lf %lf %lf %lf %lf %lf %lf %d %d\n",
                      epiint,bud1b,bud2a,bud2b,bud1c,bud3a,newepi,rule,eprule);

    while (branch==1)
    {
// perform all functions until branch is 0, indicating either branch death or
  max year has been reached
// all functions are ultimately called from the year_setup function
      num_scu=(SCUPTR *) calloc(MAXSCUS,sizeof(SCUPTR));
      num_scu[0]=(SCUPTR) calloc(1,sizeof(SCUS));
    // Initializes the SCU structure
      n++;

      if (spp==1)
      {
        if (n<90) crown=1;
        else if (n<150) crown=2;
        else if (n>=150) crown=3;
      }
      else
      {
        if (n<11) crown=1;
        else if (n<50) crown=2;
        else if(n>=50) crown=3;
      }

      year_setup();
    // Most of the functions are called in year_setup

      free_scu();

    }

    // frees the heap for the next set of parameter values
    free_space();
   }
   fclose(fpar);
  // reached end of parameter file
  }
  //fclose(rbp);
}

/**************************************run_setup******************************/
void run_setup()
{
  printf("\nArchitectural Branching Model\n\n");
  srand(time(&t));
  seed=-time(&t);
// printf("%f\n",seed);
}


/**************************************param_sample***************************/
void param_sample()
{
```

```
  FILE *fp;
  fp=fopen("c://pareto//paretoin.txt","w");
  fprintf(fp,"rba\trbb\trbc\trbepia\trbepib\n");

  double rba,rbb,rbc,rbepia,rbepib,mainyr;//,ran;
  int i;
  if(spp==1)
  {
   rba=2.5;
   rbb=1.75;
   rbc=0.75;
   rbepia=0.7;
   rbepib=0.5;
   mainyr=50;

  fprintf(fp,"%lf\t%lf\t%lf\t%lf\t%lf\t%lf\n",rba,rbb,rbc,rbepia,rbepib,mainyr)
;

/* for(i=0;i<50;i++)
  {
   rba=4*ran3(&seed);
   rbb=3*ran3(&seed);
   rbc=1*ran3(&seed);
   rbepia=2*ran3(&seed);
   rbepib=0.7*ran3(&seed);

  fprintf(fp,"%lf\t%lf\t%lf\t%lf\t%lf\t%lf\n",rba,rbb,rbc,rbepia,rbepib,mainyr)
;
  }

   for(i=0;i<20;i++)
   {
    rba=2.5;
    rbb=1.5;
    rbc=0.5;
    rbepia=0.3;
    rbepib=0.4;
    mainyr=80*ran3(&seed);
    fprintf(fp,"%f\t%f\t%f\t%lf\t%lf\t%lf\n",rba,rbb,rbc,rbepia,rbepib,mainyr);
   }

   for(i=0;i<20;i++)
   {
    rba=3.0*ran3(&seed);
    rbb=1.75;
    rbc=0.75;
    rbepia=0.7;
    rbepib=0.5;
    mainyr=50;
    fprintf(fp,"%f\t%f\t%f\t%lf\t%lf\t%lf\n",rba,rbb,rbc,rbepia,rbepib,mainyr);
   }

   for(i=0;i<20;i++)
   {
    rba=2.5;
    rbb=3*ran2(&ranseed);
    rbc=0.75;
    rbepia=0.7;
    rbepib=0.5;
    mainyr=50;
```

```
  fprintf(fp,"%f\t%f\t%f\t%lf\t%lf\t%lf\n",rba,rbb,rbc,rbepia,rbepib,mainyr);
   }

   for(i=0;i<20;i++)
   {
    rba=2.5;
    rbb=1.75;
    rbc=3*ran2(&ranseed);
    rbepia=0.7;
    rbepib=0.5;
    mainyr=50;
    fprintf(fp,"%f\t%f\t%f\t%lf\t%lf\t%lf\n",rba,rbb,rbc,rbepia,rbepib,mainyr);
   }

   for(i=0;i<20;i++)
   {
    rba=2.5;
    rbb=1.75;
    rbc=0.75;
    rbepia=3*ran3(&seed);
    rbepib=0.5;
    mainyr=50;
    fprintf(fp,"%f\t%f\t%f\t%lf\t%lf\t%lf\n",rba,rbb,rbc,rbepia,rbepib,mainyr);
   }*/
  }

  else
  {
   rba=3;
   rbb=2.0;
   rbc=1.0;
   rbepia=0.3;
   rbepib=0.4;
   fprintf(fp,"%lf\t%lf\t%lf\t%lf\t%lf\n",rba,rbb,rbc,rbepia,rbepib);

/*   for(i=0;i<10;i++)
   {
    rba=3.0*ran3(&seed);
    rbb=1.5;
    rbc=0.5;
    rbepia=0.3;
    rbepib=0.4;
    fprintf(fp,"%f\t%f\t%f\t%lf\t%lf\n",rba,rbb,rbc,rbepia,rbepib);
   }
   for(i=0;i<10;i++)
   {
    rba=3.0;
    rbb=3*ran3(&seed);
    rbc=1.0;
    rbepia=0.3;
    rbepib=0.4;
    fprintf(fp,"%f\t%f\t%f\t%lf\t%lf\n",rba,rbb,rbc,rbepia,rbepib);
   }

   for(i=0;i<10;i++)
   {
    rba=3.0;
    rbb=1.5;
    rbc=3*ran3(&seed);
```

```
     rbepia=0.3;
     rbepib=0.4;
     fprintf(fp,"%f\t%f\t%f\t%lf\t%lf\n",rba,rbb,rbc,rbepia,rbepib);
    }*/
  }
  fclose(fp);
}
/**********************************year_setup******************************/
void year_setup()
{
  printf("\nPop %d:Beginning year %d\n",pop,n);
  if (n>=MAXYR)
  {
   printf("MAXYEAR\n");
   branch=0;
  // if past MAXYEAR, simulation ends
  }

  if(rb_a>4||rb_b>4)
  {
   branch=0;
   printf("parameters out of range\n");
  }

  else if(rb_c>4||alpha>8)
  {
   branch=0;
   printf("parameters out of range\n");
  }
// establishes parameter limits


  out_filenaming(); // establish name of file to be written to this year
  in_filenaming();  // establish name of file to be read this year--should
                          correspond to previous year's outfile
  if (n==2)
  {
   // initialize the shoot data structure
   shoot=(SEGPTR *) calloc(MAXSEGS,sizeof(SEGPTR));

   shoot[0]=(SEGPTR) calloc(1,sizeof(SEG));
//every year need to allocate this memory, due to free_space

   shoot_ini();
// fills in the information for the first year's growth--model begins with
  second year

   nseg=1;
   segNum=1;
   scuNum=1;
  // initialize counters

   int i=0;
   br_length=shoot[1]->y2;

// defines the total branch length the first year to be the length of the first
  shoot
  }

  else
```

```
  {
   read_scu();
  // reads in SCU information from previous year
   find_length(1);
  // establishes the length of the branch
  }
  mort_pretips();
// calculates the number of active tips, used to determine branch mortality

  make_sons();      //all of the current year's growth begins here
// if(nseg>200000) branch=0;
// prevents monstrous branches during sensitivity and seed analyses
  mort_posttips();
  scu_tally();
// tests for SCU independence and counts the SCUs

  write_segs(sgsout,mortplot,sgsplot);
  write_scu();

  if(branch==0) crit();

  FILE *rbp;
  rbp=fopen("c:\\rb.txt","a");
  fprintf(rbp,"%d\t%d\t%d\t%d\n",pop,n,pretip,posttip);
  fclose(rbp);

// file rb.txt stores the pre and post-tip data for potential analysis
}

/***********************************shoot_ini**********************************/
void shoot_ini()
{
  // fills in the first segment
  int j;

  double iniage;
  iniage=-1;


  shoot[1]=(SEGPTR) calloc(1,sizeof(SEG));

  if(spp==1) shoot[1]->length=3.866;    // length of shoot
  else shoot[1]->length=8.128;
  shoot[1]->segNum=1;            // numbering to keep track of segments
  shoot[1]->x1=0;
// first x-coordinate for plotting the segment: segment coordinates are
  (x1,y1),(x2,y2)
  shoot[1]->x2=0;                // second x-coordinate for plotting the
segment
  shoot[1]->y1=0;                // first y-coordinate for plotting the segment
  shoot[1]->y2=3.866;            // second y-coordinate for plotting the
segment
  shoot[1]->fol=0.035;     // initial foliage mass based on average foliage mass
  shoot[1]->year=1;
// year shoot was formed--to calculate age of shoot each year
  shoot[1]->parent=0;            // parent shoot--this shoot had no parent
  shoot[1]->order=1;             // order of shoot
  shoot[1]->theta=1.57;
// branching angle--this shoot is perpendicular to horizontal.
// Used to determine the angles of son shoots
```

```
  shoot[1]->active=1;            // flag for whether shoot can produce new
shoots
  shoot[1]->mort=0;
// flag for whether the shoot has live foliage (0 = live foliage, 1 = no live
  foliage
  shoot[1]->SCUnum=1;            // a member of the first SCU
  shoot[1]->SCUage=1;            // SCU formed in year 1
  shoot[1]->SCUgen=1;            // SCU of first generation
  shoot[1]->SCUord=1;
  shoot[1]->age=0;        // a current-year shoot, age is 0
  shoot[1]->gen=1;        // a first generation shoot
  shoot[1]->epi=0;        // flagged as not an epi
  shoot[1]->init=0;       // flagged as not an initial epi
  shoot[1]->distout=0;
  shoot[1]->brorder=1;
  shoot[1]->dor=4;

  shoot[1]->area=30; //*FIX with real data!!!
  shoot[1]->nson=3;
  shoot[1]->dorage=iniage;

  for (j=0;j<MAXRB;j++)
  {
// the son array keeps track of daughter shoots--for now 4
  (1 extension, 2 lateral and 1 dormant bud)
// 0 means active bud, 4 means inactive bud, else contains the segNum
  (or epiNum) of the daughter shoot
// the first shoot always has three sons
   shoot[1]->son[j]=0;
  }

  nbr=1;
  shoot_fol(1);
  shoot_sna(1);
  segNum=1;
}

/*********************************make_sons*********************************/
void make_sons()
{

  for(nbr=1;nbr<=nseg;nbr++) // loop through all of the segments
  {
   if (shoot[nbr])  // test to make sure branch exists
   {
    shoot[nbr]->age=n-shoot[nbr]->year;
    if(shoot[nbr]->active==1) make_shoots();
// make shoots for this year, but only grow active shoots
    if(shoot[nbr]->mort==0)
    {
      shoot_fol(nbr);
      shoot_sna(nbr);
    }

    if (n>20&&shoot[nbr]->dorage==shoot[nbr]->age) make_epini();

    if (rule==1) scu_cnt();
// renumber regular shoots only with contiguity rule
    else if (rule==0&&shoot[nbr]->epi==1) episcu_age();
// re-number shoots with the age criterion
```

```
    }
  }
  printf("%d\t",segNum);
}
/*************************************find_length******************************/
void find_length(int a)
{
// a recursive algorithm to find the end of the main axis, whose y-coordinate
is then the length of the branch
  if (shoot[a]->epi==0)
  {
   if (shoot[a]->order==1)
   {
    if (shoot[a]->SCUnum==1)
    {
      if(shoot[a]->son[0]!=0)
      {
        if(shoot[a]->son[0]!=4) find_length(shoot[a]->son[0]);
        else br_length=shoot[a]->y2;
      }
      else br_length=shoot[a]->y2;
    }
   }
  }
}


/***********************************make_epini*******************************/
void make_epini()
{
  // tests each segment for epicormic initiation, called from make_sons
  int i;
  int sidea=0;
  int sideb=0;
  int side1a=0;

  if(eprule==1) // occurs only by percentage probabilities
  {
   epi_ini();  //grows an initial epicormic segment
   shoot[nbr]->dor=segNum;
//inactivates the bud, so won't repeat initiation at a later date.
  }

  else if (eprule==0)
// initiation if either of the lateral shoots is inactive at the terminus
  {
   if(shoot[nbr]->dor==4)
   {
    if(shoot[nbr]->son[1]!=0)
    {
      i=shoot[nbr]->son[1];

      do
      {
        i=shoot[i]->son[0];
        if (i==4)
        {
          if(shoot[nbr]->init==0&&shoot[shoot[nbr]->parent]->init==0)
          {
            if(shoot[shoot[shoot[nbr]->parent]->parent]->init==0)
```

```
             {
                    epi_ini();
// when son=4, then that terminal shoot is not growing
                    FILE *fgam;
                    fgam=fopen("c:\\gammaout.txt","a");
                    fprintf(fgam,"%d\t%d\n",shoot[nbr]->age,n);
                    fclose(fgam);

                    shoot[nbr]->dor=segNum;
                    shoot[nbr]->dorage=shoot[nbr]->age;
                    side1a=1;
             }
           }
         }
       }while ((i!=0)&&(i!=4));
    }

    if (side1a==0)
// if the first side is still actively growing, test the second side
    {
       if(shoot[nbr]->son[2]!=0)
       {
         i=shoot[nbr]->son[2];
         do
         {
           i=shoot[i]->son[0];
           if (i==4)
           {
             if(shoot[nbr]->init==0&&shoot[shoot[nbr]->parent]->init==0)
             {
                 if(shoot[shoot[shoot[nbr]->parent]->parent]->init==0)
                 {
                    epi_ini();
                    FILE *fgam;
                    fgam=fopen("c:\\gammaout.txt","a");
                    fprintf(fgam,"%d\t%d\n",shoot[nbr]->age,n);
                    fclose(fgam);

                    shoot[nbr]->dor=segNum;
                    shoot[nbr]->dorage=shoot[nbr]->age;
                 }
             }
           }
         }while ((i!=0)&&(i!=4));
       }
    }
   }
  }

  else if (eprule==2)
  {
   if (shoot[nbr]->age<=20&&shoot[nbr]->dor==4)
   {
    if(shoot[nbr]->son[1]!=0)
    {
       i=shoot[nbr]->son[1];
       do
       {
         i=shoot[i]->son[0];
         if (i==4)
```

```
        {
          sidea=1;
        }
      }while ((i!=0)&&(i!=4));

      if (sidea==1)
      {
        if(shoot[nbr]->son[2]!=0)
        {
          i=shoot[nbr]->son[2];
          do
          {
            i=shoot[i]->son[0];
            if (i==4)
            {
              if(shoot[nbr]->init==0&&shoot[shoot[nbr]->parent]->init==0)
              {
                 if(shoot[shoot[shoot[nbr]->parent]->parent]->init==0)
                 {
                  epi_ini();
                  shoot[nbr]->dor=segNum;
                  shoot[nbr]->dorage=shoot[nbr]->age;
                  FILE *fgam;
                  fgam=fopen("c:\\gammaout.txt","a");
                  fprintf(fgam,"%d\t%d\n",shoot[nbr]->age,n);
                  fclose(fgam);
                 }
              }
            }
          }while ((i!=0)&&(i!=4));
        }
      }
    }
   }
  }
}

/*********************************epi_ini**********************************/
void epi_ini()
{
// fills in the information for a newly initiated epicormic shoot
  int j;

  segNum+=1;
  shoot[segNum]=(SEGPTR) calloc(1,sizeof(SEG));

  shoot[segNum]->segNum=segNum;
  shoot[segNum]->order=1;
  shoot[segNum]->parent=nbr;
  shoot[segNum]->x1=shoot[nbr]->x2;
  if (n%2==0) shoot[segNum]->theta=shoot[nbr]->theta-0.1;
//want it on top of the branch (towards the main stem),

  else shoot[segNum]->theta=shoot[nbr]->theta+0.1;
// shoot[segNum]->theta=1.57;

  shoot[segNum]->length=1.0;  // length?  same as initial for now
  shoot[segNum]->x2=shoot[segNum]->x1+cos(shoot[segNum]->theta)*
                                                        shoot[segNum]->length;
  shoot[segNum]->y1=shoot[nbr]->y2;
```

```
  shoot[segNum]->y2=shoot[segNum]->y1+sin(shoot[segNum]->theta)*
                                                      shoot[segNum]->length;
  shoot[segNum]->active=1;
  shoot[segNum]->fol=.035;
  shoot[segNum]->year=n;
  shoot[segNum]->mort=0;
  shoot[segNum]->gen=shoot[nbr]->gen+1;
  shoot[segNum]->age=0;
  shoot[segNum]->epi=1;
  shoot[segNum]->init=1;
  shoot[segNum]->distout=shoot[nbr]->distout;
  shoot[segNum]->dor=4;
  shoot[segNum]->dorage=18;

  for (j=0;j<MAXRB;j++)
  {
   shoot[segNum]->son[j]=4;
  }
  shoot_fol(segNum);
  shoot_sna(segNum);

  make_inibud();


  shoot[segNum]->SCUnum=shoot[nbr]->SCUnum;
  shoot[segNum]->SCUage=shoot[nbr]->SCUage;
  shoot[segNum]->SCUgen=shoot[nbr]->SCUgen;
  shoot[segNum]->brorder=1;
}
/****************************make_youngbuds***********************************/
void make_youngbuds()
{
  double epirb,rbordc;
  // this function flags buds for different fates: son[0]=extension,
son[1or2]=lateral growth, son[3+] not modeled
  // flags: 4=inactive, 0=potential growth/dormancy.
  // When not flagged as 4, the flag is replaced by the number of the daughter
shoot when one is grown
  // called from make_sons
  int j;
  double k;

  if (shoot[segNum]->order==1)
  {
   if(shoot[shoot[segNum]->parent]->init==1)
   {
    if(shoot[segNum]->gen<=3) k=poisdev(rbepi_a,&ranseed);
    else
    {
      epirb=rbepi_a*3/shoot[segNum]->gen;
      k=poisdev(epirb,&ranseed);
    }
   //  k=poisdev(rbepi_a,&ranseed);
    if(k<MAXRB)
    {
      if (k!=0) for(j=0;j<k;j++)
      {
        shoot[segNum]->son[j]=0;
      }
      shoot[segNum]->nson=k;
```

```
    }
    else
    {
      shoot[segNum]->nson=MAXRB;
      for(j=0;j<MAXRB;j++)
      {
        shoot[segNum]->son[j]=0;
      }
    }
   }
   else
   {
    if(spp==1)
    {
   //   k=poisdev(rb_a,&ranseed);
      if(shoot[segNum]->epi==0&&n<yr) k=3;
      else k=poisdev(rb_a,&ranseed);
    }
    else
    {
      if(crown!=3) k=3;
      else k=poisdev(rb_a,&ranseed);
    }
//    k=poisdev(rb_a,&seed);

// nsons is limited by the MAXRB, here 3
    if (k<MAXRB)
    {
      shoot[segNum]->nson=k;
      if (k!=0) for(j=0;j<k;j++)
// creates the number of sons as defined by k, with extension given priority
      {
        shoot[segNum]->son[j]=0;
      }
    }
    else
    {
      shoot[segNum]->nson=MAXRB;
      for(j=0;j<MAXRB;j++)
// creates the number of sons as defined by k, with extension given priority
      {
        shoot[segNum]->son[j]=0;
      }
    }

   }

  }
  else if(shoot[segNum]->order==2)
  {
   if(shoot[shoot[segNum]->parent]->init==1)
   {
    k=poisdev(rbepi_b,&ranseed);

    if(k<MAXRB)
    {
      shoot[segNum]->nson=k;
      if (k!=0) for(j=0;j<k;j++)
      {
        shoot[segNum]->son[j]=0;
```

```
      }
    }
    else
    {
      shoot[segNum]->nson=MAXRB;
      for(j=0;j<(MAXRB);j++)
      {
        shoot[segNum]->son[j]=0;
      }
    }
   }

   else
   {
    if(spp==1)// k=poisdev(rb_b,&ranseed);
    {
      k=poisdev(rb_b,&ranseed);
    }
    else k=poisdev(rb_b,&ranseed);

    if (k<MAXRB)
    {
      shoot[segNum]->nson=k;
      if (k!=0) for(j=0;j<k;j++)
// creates the number of sons as defined by k, with extension given priority
      {
        shoot[segNum]->son[j]=0;
      }
    }

    else
    {
      shoot[segNum]->nson=MAXRB;
      for(j=0;j<MAXRB;j++)
// creates the number of sons as defined by k, with extension given priority
      {
        shoot[segNum]->son[j]=0;
      }
    }
   }
  }
  else if(shoot[segNum]->order>=3)
  {
   rbordc=3*rb_c/shoot[segNum]->order;
   k=poisdev(rbordc,&ranseed);
//  k=poisdev(rb_c,&ranseed);

   if (k<MAXRB)
   {
    shoot[segNum]->nson=k;
    if (k!=0) for(j=0;j<k;j++)
// creates the number of sons as defined by k, with extension given priority
    {
      shoot[segNum]->son[j]=0;
    }
   }
   else
   {
    shoot[segNum]->nson=MAXRB;
    for(j=0;j<MAXRB;j++)
```

```
// creates the number of sons as defined by k, with extension given priority
    {
      shoot[segNum]->son[j]=0;
    }
   }
  }
}
/********************************make_inibuds********************************/
void make_inibud()
{
  int j;
  double k,epirb;

  if (shoot[segNum]->gen<=3) epirb=rbepi_a;
  else epirb=rbepi_a*3/shoot[segNum]->gen;
//  k=poisdev(rbepi_a,&seed);
  k=poisdev(epirb,&ranseed);
  if(k<MAXRB)
  {
   shoot[segNum]->nson=k;
   if(k!=0) for(j=0;j<k;j++)
   {
    shoot[segNum]->son[j]=0;
// for newly initiated epi's, test for 2 years whether they will get going
// to begin basis of new SCU
   }
  }
  else
  {
   shoot[segNum]->nson=MAXRB;

   for(j=0;j<MAXRB;j++)
   {
    shoot[segNum]->son[j]=0;
   }
  }
}
/******************************make_shoots*******************************/
void make_shoots()
{
// once the buds are formed, this function fills in their fates (extension,
  either lateral side, dormancy)
  if(shoot[nbr]->son[0]==0)
  {
   segNum+=1;
//add a segment, allocate memory, and grow it according to the rules for its
  type
   shoot[segNum]=(SEGPTR) calloc(1,sizeof(SEG));
   shoot_extension();
   shoot[nbr]->son[0]=segNum;
  }
  if (shoot[nbr]->son[1]==0)
  {
   segNum+=1;
   shoot[segNum]=(SEGPTR) calloc(1,sizeof(SEG));
   shoot_lateral(1);
// the integer argument places the shoot on either side of its parent shoot

   shoot[nbr]->son[1]=segNum;
  }
```

```
  if(shoot[nbr]->son[2]==0)
  {
   segNum+=1;
   shoot[segNum]=(SEGPTR) calloc(1,sizeof(SEG));
   shoot_lateral(2);
   shoot[nbr]->son[2]=segNum;
  }
  shoot[nbr]->active=0;
//once the shoot has produced sons, it can no longer grow
}

/******************************shoot_extension*******************************
***/
void shoot_extension()
{
  // fills in information for the extension daughter shoot, called from
make_shoots
  int j;
  double l_frac;//,wtl;
  double iniage;

  if (spp==1) iniage=ceil(expdev(alpha,beta,&ranseed));
  else iniage=-1;
// if (iniage>20) iniage=-1;

  FILE *fgam;
  fgam=fopen("c:\\gammaout.txt","a");
  fprintf(fgam,"%lf\t%d\n",iniage,n);
  fclose(fgam);

  l_frac=shoot[nbr]->y2/br_length; // fraction the current shoot is relative to
total length of the branch
// Used to determine growth potential, as a substitute for within-tree shading

  shoot[segNum]->segNum=segNum;
  shoot[segNum]->order=shoot[nbr]->order;
  shoot[segNum]->parent=nbr;
  shoot[segNum]->x1=shoot[nbr]->x2;
  shoot[segNum]->theta=shoot[nbr]->theta;

  if(spp==1)
  {
   if(shoot[nbr]->init==1) shoot[segNum]->length=1.5;
   else
   {
    if(shoot[shoot[nbr]->parent]->init==1) shoot[segNum]->length=2.0;
    else
    {
      if(shoot[shoot[shoot[nbr]->parent]->parent]->init==1) shoot[segNum]-
>length=3.6;
      else shoot[segNum]->length=shoot[nbr]->length;
    }
   }
  }
  else
  {
   if(n<25) shoot[segNum]->length=shoot[nbr]->length;
   else shoot[segNum]->length=6.175;
  }
```

```
  shoot[segNum]->x2=shoot[segNum]->x1+cos(shoot[segNum]-
>theta)*shoot[segNum]->length;
  shoot[segNum]->y1=shoot[nbr]->y2;
  shoot[segNum]->y2=shoot[segNum]->y1+sin(shoot[segNum]->theta)*shoot[segNum]-
>length;
  shoot[segNum]->active=1;
  shoot[segNum]->year=n;
  shoot[segNum]->mort=0;
  shoot[segNum]->SCUnum=shoot[nbr]->SCUnum;
  shoot[segNum]->SCUage=shoot[nbr]->SCUage;
  shoot[segNum]->SCUgen=shoot[nbr]->SCUgen;
  shoot[segNum]->SCUord=shoot[nbr]->SCUord;
  shoot[segNum]->age=0;
  shoot[segNum]->gen=shoot[nbr]->gen;
  shoot[segNum]->epi=shoot[nbr]->epi;
  shoot[segNum]->init=0;
  shoot[segNum]->distout=shoot[nbr]->distout;
  shoot[segNum]->brorder=shoot[nbr]->brorder;
  shoot[segNum]->dor=4;

  shoot[segNum]->nson=0;
  shoot_fol(segNum);

  if (shoot[segNum]->order==1) shoot[segNum]->dorage=iniage;
  else shoot[segNum]->dorage=-1;
  for (j=0;j<MAXRB;j++)
  {
   shoot[segNum]->son[j]=4;
  }

  shoot_sna(segNum);

  make_youngbuds();
}

/*******************************shoot_lateral1*********************************
/
void shoot_lateral(int side)
{
  // fills in information for a lateral shoot, called from make_shoots
  int j;
  int q1,q2;

  double lrat,ang;//,wtl;

  shoot[segNum]->dorage=-1;

  shoot[segNum]->segNum=segNum;
  shoot[segNum]->order=shoot[nbr]->order+1;
  shoot[segNum]->parent=nbr;
  shoot[segNum]->x1=shoot[nbr]->x2;

  if (spp==1)
  {
   if (crown==1)
   {
    q1=-1;
    q2=-1;
   }
```

```
 else if(crown==2)
 {
  q1=1;
  q2=-1;
 }

 else if(crown==3)
 {
  q1=0;
  q2=2;
 }
 ang=(1.57-(60.5253-1.2327*shoot[nbr]->length-1.1471*q1+
                                               0.4257*q2)*3.14/180);
 if (side==1) shoot[segNum]->theta=shoot[nbr]->theta-ang;
 else shoot[segNum]->theta=shoot[nbr]->theta+ang;
 lrat=0.9446+0.0703*q1+0.0163*q2-0.0758*shoot[nbr]->order;
 shoot[segNum]->length=shoot[nbr]->length*lrat;
}

else
{
 if (crown==1)
 {
  ang=(1.57-(54.58+0.5848*shoot[nbr]->length)*3.14/180);
  if (side==1) shoot[segNum]->theta=shoot[nbr]->theta-ang;
  else shoot[segNum]->theta=shoot[nbr]->theta+ang;

  lrat=exp(-0.81+0.0082*ang);
  shoot[segNum]->length=shoot[nbr]->length*lrat;
 }

 else if(crown==2)
 {
  ang=1.57-56.8*3.14/180;
  if (side==1) shoot[segNum]->theta=shoot[nbr]->theta-ang;
  else shoot[segNum]->theta=shoot[nbr]->theta+ang;

  lrat=exp(-0.1561*shoot[nbr]->order);
  shoot[segNum]->length=shoot[nbr]->length*lrat;
 }

 else if(crown==3)
 {
  ang=1.57-(64.85-1.1431*shoot[nbr]->length)*3.14/180;
  if (side==1) shoot[segNum]->theta=shoot[nbr]->theta-ang;
  else shoot[segNum]->theta=shoot[nbr]->theta+ang;

  lrat=exp(-0.9897-0.1211*shoot[nbr]->order);
  shoot[segNum]->length=shoot[nbr]->length*lrat;
 }
}


shoot[segNum]->x2=shoot[segNum]->x1+cos(shoot[segNum]->theta)*
                                                  shoot[segNum]->length;
shoot[segNum]->y1=shoot[nbr]->y2;
shoot[segNum]->y2=shoot[segNum]->y1+sin(shoot[segNum]->theta)*
                                                  shoot[segNum]->length;
shoot[segNum]->active=1;
shoot[segNum]->year=n;
```

```
  shoot[segNum]->mort=0;
  shoot[segNum]->SCUnum=shoot[nbr]->SCUnum;
  shoot[segNum]->SCUage=shoot[nbr]->SCUage;
  shoot[segNum]->SCUgen=shoot[nbr]->SCUgen;
  shoot[segNum]->SCUord=shoot[nbr]->SCUord;
  shoot[segNum]->age=0;
  shoot[segNum]->gen=shoot[nbr]->gen;
  shoot[segNum]->epi=shoot[nbr]->epi;
  shoot[segNum]->init=0;
  shoot[segNum]->distout=shoot[nbr]->distout;
  shoot[segNum]->brorder=shoot[nbr]->brorder+1;
  shoot[segNum]->dor=4;

  shoot[segNum]->nson=0;

  shoot_fol(segNum);


  for (j=0;j<MAXRB;j++)
  {
   shoot[segNum]->son[j]=4; //for eprule!=1
  }
  make_youngbuds();

  shoot_sna(segNum);
}

/************************************shoot_fol********************************/
void shoot_fol(int wrk)
{
// uses the regression relationship to calculate foliage weights per shoot
  //length of particularly aged shoots
  int folag,ind;
  double wtl;

// regression values are in mg, multiply by 1000 in final calculation to get
  total foliage on the shoot in g.
  if (shoot[wrk]->mort==0)
  {
   folag=shoot[wrk]->age;
   if(spp==1)
   {
    if(crown==1)
    {
      if (folag>4) ind=1;
      else ind=0;
      wtl=pow(8.1743+.03203*folag-1.7214*(folag-4.0)*ind,2);
    }
    else if(crown==2)
    {
      if (folag>4.75) ind=1;
      else ind=0;
      wtl=pow(7.1148+.1948*folag-1.3494*(folag-4.75)*ind,2);
    }
    else if (crown==3)
    {
      if (folag>4) ind=1;
      else ind=0;
      wtl=pow(5.9332+0.0346*folag-0.8807*(folag-4.0)*ind,2);
    }
```

```
   }
   else
   {

    if(crown==1)
    {
      if(folag>1.25) ind=1;
      else ind=0;
      wtl=exp(3.6909+1.05*folag-1.2307*(folag-1.25)*ind);
    }
    else if (crown==2)
    {
      if (folag>1.5) ind=1;
      else ind=0;
      wtl=pow(5.7817+1.2701*folag-3.2644*(folag-1.5)*ind +
                                                0.0043*shoot[wrk]->distout,2);
    }
    else if(crown==3)
    {
      if (folag>1.5) ind=1;
      else ind=0;
      wtl=pow(4.6678+1.5798*folag-2.0331*(folag-1.5)*ind,2);
    }
   }
   shoot[wrk]->fol=wtl*shoot[wrk]->length/1000;
   if(shoot[wrk]->fol<0) shoot[wrk]->mort=1;
   if(spp!=1&&shoot[wrk]->age>9) shoot[wrk]->mort=1;
  }

  if(shoot[wrk]->fol<=0||shoot[wrk]->age>10)
  {
   shoot[wrk]->mort=1;
   shoot[wrk]->area=0;
  }

  // if the shoot has no more foliage, tag it as dead
}


/*******************************shoot_sna************************************/
void shoot_sna(int wrk)
{
  int folag;
  double sna;

  folag=shoot[wrk]->age;
  if(spp==1)
  {
   if(crown==1) sna=47.33-1.43*folag+0.0191*shoot[wrk]->distout;

   else if (crown==2) sna=exp(4.34-0.04*folag-0.0003*shoot[wrk]->distout);

   else if (crown==3) sna=exp(4.48 - 0.0513*folag –
                                                  0.00053*shoot[wrk]->distout +
                                          0.000048*folag*shoot[wrk]->distout);
  }

  else
  {
   if(crown==1) sna=46.48-2.79*folag;
```

```
   else if (crown==2) sna=53.86-1.03*folag;

   else if (crown==3) sna=59.79-1.20*folag;
  }
  shoot[wrk]->area=shoot[wrk]->fol*sna;
}



/**********************************in filenaming**************************/
void in_filenaming()
{
// creates a new infilename for each year, labelled by year (same as outfile
  for previous year)
// called from year_setup
  char year[10];
  char population[10];
  sprintf(year,"%d",n-1);
  sprintf(population,"%d",pop-1);
  strcpy(sgsinfile, "c:\\segout");
  strcat(sgsinfile, year);
  strcat(sgsinfile,"pop");
  strcat(sgsinfile, population);
  strcat(sgsinfile, ".txt\0");
}

/******************************out_filenaming****************************/
void out_filenaming()
{
// create outfile names to be read in each year, as well as outfiles used for
  plotting in Splus
// called from year_setup

  char year[10];
  char population[10];
  sprintf(year,"%d",n);
  sprintf(population,"%d",pop);

  strcpy(sgsout, "c:\\pop");
  strcat(sgsout, population);
  strcat(sgsout, "segout");
  strcat(sgsout, year);
  strcat(sgsout, ".txt\0");

  strcpy(mortplot, "c:\\pop");
  strcat(mortplot, population);
  strcat(mortplot, "segmort");
  strcat(mortplot, year);
  strcat(mortplot, ".txt\0");
}

/*************************************read scu***************************/
//void read_scu(char scureadname[])
void read_scu()
{
  // reads in scu information, called from year_setup
  FILE *fp;

  fp=fopen("c:\\scu.txt","r");
```

```
  fscanf(fp,"%d %d",&scuNum,&nseg);
  fclose(fp);
  segNum=nseg;
}
/***************************write_segs*********************************/
void write_segs(char filename[],char mortfilename[], char plotfilename[])
{

   int i,dorctr,livctr,epbrctr,epscuctr,main_axis;//,k;
   double folarea=0;
   int maxord=0;
   dorctr=0;
   livctr=0;
   epbrctr=0;
   epscuctr=0;
   main_axis=0;

   FILE *fp;
   FILE *dorfp;
   FILE *livfp;
   FILE *mortfp;
   fp=fopen(filename,"w");
// stores all data information for foliage-bearing shoots
   livfp=fopen("c:\\liveshoots.txt","a");
   dorfp=fopen("c:\\dormant.txt","a");

   mortfp=fopen(mortfilename,"w");
// stores data for plotting non-foliage-bearing shoots
//   fprintf(fp,"x1\tx2\ty1\ty2\tSCUnum\tgen\tlength\tangle\tsegNUM\tparent\t
              year\torder\tmort\tSCUgen\tage\tepi\tinit\tgen\tson0\tson1\tson2\
              tSCUage\tdor\tdorage\tnsons\tarea\tfol\n");


   for(i=1;i<=segNum;i++)
   {
    if(shoot[i])
    {
      if (shoot[i]->dor!=4) dorctr++;
      if (shoot[i]->mort==0)
      {
        if (shoot[i]->order==1&&shoot[i]->epi==0) main_axis=1;

        fprintf(fp,"%.3f\t%.3f\t%.3f\t%.3f\t%d\t%d\n",shoot[i]->x1,
                         shoot[i]->x2,shoot[i]->y1,shoot[i]->y2,shoot[i]-
                         >SCUnum,shoot[i]->gen);
//      fprintf(fp,"%d\t%d\t%d\t%d\t%d\t%d\t%d\t%d\t%d\t%lf\n",
                           shoot[i]->segNum,shoot[i]->SCUnum,shoot[shoot[i]-
                           >parent]->order,shoot[i]->parent,shoot[i]-
                           >order,shoot[i]->son[0],shoot[i]->son[1],shoot[i]-
                           >son[2],shoot[i]->init,shoot[i]->theta);
/*      fprintf(fp,"%lf\t%lf\t%d\t%d",shoot[i]->length,
                           shoot[i]->theta,shoot[i]->segNum,shoot[i]->parent);
        fprintf(fp,"\t%d\t%d\t%d\t%d\t%d\t%d\t%d\t%d\t",
                           shoot[i]->year,shoot[i]->order,shoot[i]-
                           >mort,shoot[i]->SCUgen,shoot[i]->age,shoot[i]-
                           >epi,shoot[i]->init,shoot[i]->gen);
        fprintf(fp,"%d\t%d\t%d\t",shoot[i]->son[0],shoot[i]->son[1],
                           shoot[i]->son[2]);
        fprintf(fp,"%d\t",shoot[i]->SCUage);
        fprintf(fp,"%d\t%lf\t%lf\t",shoot[i]->dor,shoot[i]->dorage,
```

```
                              shoot[i]->nson);
         fprintf(fp,"%lf\t%lf\n",shoot[i]->area,shoot[i]->fol);
*/

         livctr++;
         folarea+=shoot[i]->area;
         if(shoot[i]->epi==1) epbrctr++;
         if(shoot[i]->gen!=shoot[i]->SCUgen) epscuctr++;
       }
       else if(shoot[i]->order==1)
                                fprintf(mortfp,"%.3f\t%.3f\t%.3f\t%.3f\t%d\n",
                                shoot[i]->x1,shoot[i]->x2,shoot[i]-
                                >y1,shoot[i]->y2,shoot[i]->SCUnum);

     }
    }
    fclose(fp);
    fclose (mortfp);

    fprintf(dorfp,"%d\t%d\t%d\n",pop,n,dorctr);
    fclose(dorfp);
    fprintf(livfp,"%d\t%d\t%d\t%d\t%d\t%d\t%d\t%d\t%lf\n",pop,n,
                   livctr,epbrctr,epscuctr,segNum,numScu,main_axis,folarea);
    fclose(livfp);

  printf("%d\n",livctr);
  if(livctr==0)
  {
   branch=0;
   printf("No more live shoots\n");
  }
}

/************************************write scu*******************************/
//void write_scu(char scufilename[])
void write_scu()
{
  // stores the index of epi's, seg's, scu's
  FILE *fp;
  //fp=fopen(scufilename,"w");
  fp=fopen("c:\\scu.txt","w");
  fprintf(fp,"%d\t%d\n",scuNum,segNum);
  fclose(fp);
}

/***************************free_space for i/o**********************/
void free_space()
{
  // frees the data structure at the end of each population run
  int i;
  for (i=0;i<=segNum;i++)
  {
   free((char *)shoot[i]);
  }
  free((char *)shoot);
}

/*****************************SCU determination********************/
void scu_cnt()
{
```

```
// called only if rule=1 (contiguity), else there is no re-numbering of
regular
  shoots
  if(nbr>1)
  {
   if (shoot[nbr]->age==10)
   {
    if (shoot[nbr]->init==0)
    {

// for a non-initiated shoot, the parent shoot must be of greater order than
  its parent
      if ((shoot[nbr]->order)!=(shoot[shoot[nbr]->parent]->order))
      {
        shoot[nbr]->lin=0;
        scushoot_cnt(nbr);

        if(shoot[nbr]->lin>10) add_scu();
        else
        {
          shoot[nbr]->SCUnum=0;
          scu_loop(nbr);
        }
      }
    }
    else //for epis the order plus is automatically fulfilled
    {
      shoot[nbr]->lin=0;
      scushoot_cnt(nbr);
      if(shoot[nbr]->lin>10) add_scu();
      else
      {
        shoot[nbr]->SCUnum=0;
        scu_loop(nbr);
      }
    // if it is an initiated shoot, then it only needs to be dead
    }
   }
  }
}


/**************************scushoot_cnt**********************************/
void scushoot_cnt(int wrk)
{
  int i;

  if(shoot[wrk]->dor!=4)
  {
   if(shoot[wrk]->dor!=0) shoot[nbr]->lin+=1;
  }
  for (i=0;i<=3;i++)
  {
   if(shoot[wrk]->son[i]!=0)
   {
    if(shoot[wrk]->son[i]!=4)
    {
    //printf("%lf",idx);
      //idx+=1;
      shoot[nbr]->lin+=1;
```

```
      scushoot_cnt(shoot[wrk]->son[i]);
    }
   }
  }

}

/**********************************add SCU**********************************/
void add_scu()
{
  // allocates memory for a new SCU in the data structure
  scuNum+=1; // index of total SCU's
  ag=n;
  gn=shoot[nbr]->gen; // keeps track of generation of the new SCU
  ord=shoot[nbr]->brorder; // keeps track of the SCU order

  scu_out(0,nbr);

  shoot[nbr]->SCUnum=scuNum;
// these three store SCU info in the segment data structure
  shoot[nbr]->SCUage=ag;
  shoot[nbr]->SCUgen=gn;
  shoot[nbr]->distout=dout;
  shoot[nbr]->SCUord=ord;
  shoot[nbr]->order=1;

  scu_loop(nbr);
}

/***************************episcu rule0 (by age)***************************/
void episcu_age()
{
  if (shoot[nbr]->init==1)
  {
   if (shoot[nbr]->age==10)
   {
    shoot[nbr]->lin=0;
    scushoot_cnt(nbr);
    if(shoot[nbr]->lin>10) add_scu();
    else
    {
      shoot[nbr]->SCUnum=0;
      scu_loop(nbr);
    }
   }
  }
}

/******************************scu_out recursion******************/
void scu_out(double d,int a)
{
  if(a!=1)
  {
   d+=shoot[shoot[a]->parent]->length;
   scu_out(d,shoot[a]->parent);
  }
  else dout=d;
}
```

```
/********************************scu_loop recursion********************/
void scu_loop(int wrk)
{
// a recursion loop to step through all of the daughter shoots in the newly
  forming SCU; calls itself as well as the epi version for its epicormic sons
  int j;
  for (j=0;j<=3;j++)
  {
   if((shoot[wrk]->son[j]!=4)&&(shoot[wrk]->son[j]!=0))
   {
    if(shoot[wrk]->SCUnum!=0)
    {
      if (shoot[shoot[wrk]->son[j]])
      {
        scuseg_num(shoot[wrk]->son[j]);
        scu_loop(shoot[wrk]->son[j]);

      }
    }
    else
    {
      shoot[shoot[wrk]->son[j]]->SCUnum=0;
      scu_loop(shoot[wrk]->son[j]);
    }

   }
  }
}

/*************************************scuseg_num******************************/
void scuseg_num(int a)
{
  // called from the recursive loops, fills in the same info for all the shoots
in the SCU
  shoot[a]->SCUnum=scuNum;
  shoot[a]->SCUage=ag;
  shoot[a]->SCUgen=gn;
  shoot[a]->distout=dout;
  shoot[a]->SCUord=ord;
  if(rule==1)
  {
   if(a==shoot[shoot[a]->parent]->son[0]) shoot[a]->order = shoot[shoot[a]-
>parent]->order;
   else shoot[a]->order = shoot[shoot[a]->parent]->order+1;
  }
}

/**********************************crit1*************************************/
void crit()
{
// calculates desired model outputs at end of model run
  int k;
  double scuepitot=0;
  double scushttot=0;
  double segscutot=0;
  double shttot=0;
  double epitot=0;
  double areatot=0;
  double wttot=0;
```

```
  double crit1,crit2,crit3,crit4;
  for(k=1;k<=segNum;k++)
  {
   if (shoot[k]->mort==0)
   {
    shttot+=1;
    if (shoot[k]->epi==1) epitot+=1;
    areatot+=shoot[k]->area;
    wttot+=shoot[k]->fol;
   }
  }

  crit2=areatot;
  crit1=shttot;
  crit3=wttot;
  crit4=numScu;

  FILE *fp;
  fp=fopen("c:\\pareto\\critout.txt","a");
  fprintf(fp,"%d\t%d\t%lf\t%lf\t%lf\t%lf\n",pop,n,crit1,crit2,crit3,crit4);
  fclose(fp);
}

/**********************************mort pretips**************************/
void mort_pretips()
{
// counts the number of active tips before the year's growth
  pretip=0;
  int i;
  for(i=1;i<=nseg;i++)
  {
   if(shoot[i]->active==1) pretip++;
  }
}
/**********************************mort post tips***********************/
void mort_posttips()
{
  // counts the number of active shoot tips after the year's growth
  posttip=0;
  int i;
  for(i=1;i<=segNum;i++)
  {
   if(shoot[i]->active==1) posttip++;
  }
}



/**********************************scu_tally*********************************/
void scu_tally()
{
// tallies the SCUs modified and created this year and updates the demography
  changes of SCUs (changes in shoot numbers due to growth and mortality)
  FILE *fp;
  fp=fopen("c:\\numscu.txt","a");
  numScu=0; // start with 0 SCUs, add to this total as find alive SCUs
  SCUNum[0]=0;
  int i,k;
  for(i=1;i<=segNum;i++)
// loop through all segments to determine the shoot make-up of the SCU (i.e.
```

```
  numbers of regular and epicormic shoots
  {
   if (shoot[i]->mort==0) scu_search(i,0);
// for alive shoots, search for its SCU, beginning search with "SCU[0]", which
  doesn't exist, just gives a starting point

  }
  for(k=1;k<=numScu;k++)
  {
   for(i=0;i<10;i++)
   {
    fprintf(fp,"%d\t%d\t%d\t%d\t%d\t%d\t%d\n",num_scu[k]->pop,n,i,
                          num_scu[k]->gen,num_scu[k]->scuNum,num_scu[k]-
                          >regagcnt[i],num_scu[k]->epagcnt[i]);
   }
   // prints all of the updated SCU demographic info to a file
  }

  fclose(fp);
}
/********************************scu_search***********************************/
void scu_search(int p,int q)
// p is the index of the shootworking on, q is the SCU index
{
  int z;
// a recursion to update the SCU demography; each round of recursions involves
  a single shoot
  if(shoot[p]->SCUnum==SCUNum[q])
// this function searches through the SCU array, until the SCUnum of the shoot
  matches an SCU in the array.
  {
   if(shoot[p]->gen==num_scu[q]->gen)
   {
    num_scu[q]->regagcnt[shoot[p]->age]++;
   }
   else
   {
    num_scu[q]->epagcnt[shoot[p]->age]++;
   }
  }
  else if(q==numScu)
// if the SCU index reaches the highest newly tallied numScu, then add an SCU,
  fill in values, and exit the recursion
  {
   numScu++;
   num_scu[numScu]=(SCUPTR) calloc(1,sizeof(SCUS));
// allocates memory for a new SCU; this structure is freed and read-in every
  year of the simulation
   num_scu[numScu]->gen=shoot[p]->gen;
   num_scu[numScu]->pop=pop;
   num_scu[numScu]->year=n;
   num_scu[numScu]->scuNum=shoot[p]->SCUnum;
   num_scu[numScu]->distout=shoot[p]->distout;
   num_scu[numScu]->age=shoot[p]->SCUage;
   SCUNum[numScu]=shoot[p]->SCUnum;
// identifies this spot in the array with the SCUnum of the shoot.

   for(z=0;z<10;z++)
   {
    if(shoot[p]->age==z) num_scu[numScu]->regagcnt[z]=1;
```

```
     else num_scu[numScu]->regagcnt[z]=0;
     num_scu[numScu]->epagcnt[z]=0;
    }

  }
  else
// if the SCU index has not looped through the entire tallied numScu, then keep
  searching by increasing the SCU index by 1
  {
   q++;
   scu_search(p,q);
  }
}

/************************************free_scu*********************************/
void free_scu()
{
// once the updated SCU information is written to a file, the scu data
  structure is freed, to be read in the next year
  int i;
  for(i=0;i<=numScu;i++)
  {
   free((char *)num_scu[i]);
  }
  free((char *)num_scu);
}

/************************************factorial********************************/
double factorial(int b)
{
  double value=b;
  if(b<=1) value=1;

  else
  {
   while(b!=1)
   {
    value=value*(b-1);
    b=b-1;
   }
  }
  return (value);
}

/**************ran3: from Numerical Recipes in C, 2nd ed, pg. 283**********/
double ran3(long *idum)
// returns a uniform random deviate from 0-1. Set idum to any negative value to
  initialize or reinitialize the sequence
{
  static int inext,inextp;
  static long ma[56];
  static int iff=0;
  long mj,mk;
  int i,ii,k;

  if(*idum<0||iff==0)
  {
   iff=1;
   mj=labs(MSEED-labs(*idum));
   mj %= MBIG;
```

```
   ma[55]=mj;
   mk=1;

   for(i=1;i<=54;i++)
   {
    ii=(21*i) % 55;
    ma[ii]=mk;
    mk=mj-mk;
    if(mk<MZ) mk+=MBIG;
    mj=ma[ii];
   }

   for(k=1;k<=4;k++)
    for(i=1;i<=55;i++)
    {
      ma[i] -= ma[1+(i+30) % 55];
      if (ma[i]<MZ)ma[i]+=MBIG;
    }

    inext=0;
    inextp=31;
    *idum=1;
  }

  if (++inext==56) inext=1;
  if (++inextp==56) inextp=1;
  mj=ma[inext]-ma[inextp];
  if (mj<MZ) mj+=MBIG;
  ma[inext]=mj;

  FILE *ranfp;
  ranfp=fopen("C:\\rannum.txt","a");
  fprintf(ranfp,"%d\t%lf\n",n,mj*FAC);
  fclose(ranfp);

  return mj*FAC;

}


/***********ran2, from Numerical recipes in C, pp 282**********************/
double ran2(long *idum)
{
  int j;
  long k;
  static long idum2=123456789;
  static long iy=0;
  static long iv[NTAB];
  double temp;

  if (*idum<=0)
  {
   if (-(*idum) <1) *idum=1;
   else *idum = -(*idum);
   idum2=(*idum);

   for(j=NTAB+7;j>=0;j--)
   {
    k=(*idum)/IQ1;
    *idum=IA1*(*idum-k*IQ1)-k*IR1;
```

```
    if(*idum<0) *idum+=IM1;
    if(j<NTAB) iv[j]=*idum;
   }

   iy=iv[0];
  }

  k=(*idum)/IQ1;
  *idum=IA1*(*idum-k*IQ1)-k*IR1;
  if(*idum<0) *idum+=IM1;
  k=idum2/IQ2;
  idum2=IA2*(idum2-k*IQ2)-k*IR2;
  if(idum2<0) idum2+=IM2;
  j=iy/NDIV;
  iy=iv[j]-idum2;
  iv[j]=*idum;
  if(iy<1) iy+=IMM1;


  if((temp=AM*iy)>RNMX)
  {
   return RNMX;
  }

  else
  {
   return temp;
  }
}


/*****************expdev; from Numerical Recipes in C, pp 287*****************/
double expdev(int ia, double lambda, long *idum)
// Returns gamma deviates for small integer alpha as the sum of exponential
  deviates.  for alpha=1 simply an exponential deviate
{
  double gam;
  double dum=1.0;
  int j;

  //for (j=1;j<=ia;j++) dum*=ran3(idum);
  for (j=1;j<=ia;j++) dum*=ran2(idum);


  gam=-lambda*log(dum*lambda);
  return gam;
}

/*********************poisdev; from Numerical Recipes in C, pp 294**********/
double poisdev(double xm, long *idum)
// returns as a floating point number an integer value that is a random deviate
  drawn from a Poisson distribution with
// lambda=xm, using ran3 as a source of uniform random deviates; uses rejection
  method as outlined in book
{
  static double sq,alxm,g,oldm=(-1,0);
  double em,t;//,y;

  if (xm<12.0)
  {
```

```
   if (xm!=oldm)
   {
    oldm=xm;
    g=exp(-xm);
   }

   em=-1;
   t=1.0;
   do
   {
    ++em;
   //  t*=ran3(idum);
    t*=ran2(idum);
   }
   while (t>g);
  }

  return em;
}



/************************************end model code***************************/
```

Model Header File: “mod1.h”

```
#define MAXRB 3
#define MAXSEGS 9000000
//#define MAXEPIS 1000000
#define MAXSCUS 400000
#define MAXYR 400
#define MAXDORM 2
#define MAXGEN 7

FILE *outfile;

/******************************branch structure=segs**********************/
struct segs {
  int segNum; //the segment number, may not need in this program
  int parent; //parent of this segment
  double length; //length of segment
  int gen;  //always 1, but necessary for criteria output
  double theta;     //angle of segment to its parent
  int son[MAXRB+1]; //daughter shoots of this segment, called sons for typing
ease
  int year;//year this segment was formed
  double fol; //calculated by age and crown position
  int order; //order of this shoot wrt to the SCU
  int brorder; // order ofthe shoot wrt to the branch
  int active; //indicates whether the branch is still growing
  int SCUnum; //location parameter, using isolation to determine SCU
  int SCUage;
  int SCUgen;
  int SCUord;
  double x1; //first x coordinate of segment
  double x2; //second x coordinate of segment
  double y1; //first y coordinate of segment
  double y2; //second y coordinate of segment
  int mort;//flag of mortality--when = 1, separate file, either don't print or
print with dashes
  int age;
```

```
  double area;
  int epi;
  int init;
  double distout;
  int dor;
  double dorage;
  double nson;
  int SCUfirst;
  int lin;
};

/*******************************another scu try****************************/
struct scu {
  int epagcnt[10];
  int regagcnt[10];
  int pop;
  int year;
  int gen;
  int scuNum;
  double distout;
  int age;
};

/**********************************functions**********************************/
//Program maintenance functions
void run_setup();  //before loop, to read in the data and run params
void year_setup(); //reads in previous year's data, allocates memory,creates
new segments from the previous year's buds
void in_filenaming(); // creates file names appropriate for the year and
population to be read in
void out_filenaming(); // creates outfile names appropriate for the year and
parameter population
void free_space();  //use when have i/o figured out--frees up memory of segment
structure, to be reallocated each year
void free_scu();

//Growth functions, regular shoots
void shoot_ini(); // creates the first shoot of the branch, same values for
every run
void make_shoots(); // fills in appropriate structure values for each of the
new shoots
void make_youngbuds();  // flags active buds for next year, decides how many
and which will grow
void make_sons();   // calls the functions for bud formation and shoot growth
void shoot_extension(); // fills in structure values for a shoot that is an
extension of its parent
void shoot_lateral(int side); // fills in structure values for a shoot that is
one-side lateral of its parent
lateral1, filling in the other side lateral of its parent
void shoot_fol(int wrk); // uses regression relationships to determine foliage
weight of a given shoot
void shoot_sna(int wrk); // uses regression relationships to determine foliage
area of a given shoot
void scu_cnt(); // re-numbers SCUs according to the contiguity criterion
void scuseg_num(int a); // fills in same information for all SCUs that are
renumbered as independent
void find_length(int a); // finds the length of the branch by the y2 value of
the last first order regular shoot

//Growth functions, epicormic shoots
```

```
void epi_ini(); // fills in information for an initiated epicormic shoot
void make_epini(); // tests each segment for epicormic initiation
void make_inibud();
void add_scu(); // allocates memory for a new SCU in the data structure
void scu_loop(int wrk); // a recursion loop to step through all daughter shoots
of the newly independent SCU

//Output functions
void write_segs(char filename[],char mortfilename[],char plotfilename[]); //
writes yearly output files
void write_scu(); // writes index information to be read in each year (i.e.
shoot number, scu number)
void scu_tally(); // updates and writes to file SCU demography values (i.e. epi
count, shoot count, age, etc)
void scu_search(int p,int q); // a recursion to search for the SCU to which a
shoot belongs, and update the SCU information accordingly
mortfilename[],char inimortfilename[]);
void write_scu(char scufilename[]);

// Input functions
void read_scu(); // reads in the index values from the previous year

//POMAC functions
void crit();
void episcu_age(); // re-numbers SCUs according to the age criterion and epi
origin only
void param_sample(); // creates a random sample of parameter values within
certain ranges

//mortality functions
void mort_pretips(); // counts the number of active growing tips before new
growth occurs that year
void mort_posttips(); // counts the number of active growing tips after new
growth occurs that year
void scu_out(double dout,int a);


double factorial(int b);
double expdev(int ia, double lambda, long *idum);
double poisdev(double xm, long *idum);

void scushoot_cnt(int wrk);
/* Parameter file:
epint  % probability of epicormic initiation from an epicormic or regular shoot
(thereby increasing bud generations)--an integer that when divided by 10 yields
the desired probability
ep1a % probability of extension of a first order epicormic
ep1b % probability of lateral growth of a first order epicormic or second order
regular shoot
ep2a % probability of extension of a second order epicormic or regular shoot
(for now no lateral growth of second order epicormics)
bd1b % probability of lateral growth of a first order regular shoot
bd1c % probability of formation of a dormant bud available for epicormic
initiation
bd3a % probability of extension of a third order regular shoot
newep  % probability of extension of a newly formed epicormic

  In the parameter file the values should be entered in the above order ON THE
SAME LINE, SEPARATED BY TABS
```

```
*/

/***************************************************************************/
```

Random number header file: "ran.h"

```
#define MBIG 1000000000
#define MSEED 161803398
#define MZ 0
#define FAC (1.0/MBIG)
#define PI 3.141592654

double ran3(long *idum);


#define IM1 2147483563
#define IM2 2147483399
#define AM (1.0/IM1)
#define IMM1 (IM1-1)
#define IA1 40014
#define IA2 40692
#define IQ1 53668
#define IQ2 52774
#define IR1 12211
#define IR2 3791
#define NTAB 32
#define NDIV (1+IMM1/NTAB)
#define EPS 1.2e-7
#define RNMX (1.0-EPS)

double ran2(long *idum);
```