

Defining how aging *Pseudotsuga* and *Abies* compensate for multiple stresses through multi-criteria assessment of a functional-structural model

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Summary Many hypotheses have been advanced about factors that control tree longevity. We use a simulation model with multi-criteria optimization and Pareto optimality to determine branch morphologies in the Pinaceae that minimize the effect of growth limitations due to water stress while simultaneously maximizing carbohydrate gain. Two distinct branch morphologies in the Pareto optimal space resemble *Pseudotsuga menziesii* (Mirb.) Franco and *Abies grandis* (Dougl. ex D. Don) Lindl., respectively. These morphologies are distinguished by their performance with respect to two pathways of compensation for hydraulic limitation: minimizing the mean path length to terminal foliage (*Pseudotsuga*) and minimizing the mean number of junction constrictions to terminal foliage (*Abies*). Within these two groups, we find trade-offs between the criteria for foliage display and the criteria for hydraulic functioning, which shows that an appropriate framework for considering tree longevity is how trees compensate, simultaneously, for multiple stresses. The diverse morphologies that are found in a typical old-growth conifer forest may achieve compensation in different ways. The method of Pareto optimization that we employ preserves all solutions that are successful in achieving different combinations of criteria. The model for branch development that we use simulates the process of delayed adaptive reiteration (DAR), whereby new foliage grows from suppressed buds within the established branch structure. We propose a theoretical synthesis for the role of morphology in the persistence of old *Pseudotsuga* based on the characteristics of branch morphogenesis found in branches simulated from the optimal set. (i) The primary constraint on branch growth for *Pseudotsuga* is the mean path length; (ii) as has been previously noted, DAR is an opportunistic architecture; and (iii) DAR is limited by the number of successive reiterations that can form. We show that *Pseudotsuga* morphology is not the only solution to old-growth constraints, and we suggest how the model results should be used to guide future empirical investigation based on the two contrasting morphologies and how

the morphological contrast may relate to physiological processes. Our results show that multi-criteria optimization with Pareto optimality has promise to advance the use of models in theory development and in exploration of functional~structural trade-offs, particularly in complex biological systems with multiple limiting factors.

Keywords: age-related decline, carbon limitation, hydraulic limitation, Pareto optimality, reiteration.

Introduction

There is considerable interest in understanding the physiology of aging trees: in how old trees manage to grow so large and persist to such old ages (Westing 1964, Lanner 2002), what causes net growth to decline in large trees (Gower et al. 1996, Mencuccini and Grace 1996, Ryan et al. 1997, Ryan and Yoder 1997, Bond 2000, Acker et al. 2002, Ryan et al. 2004) and in the general relationship between plant form and function as both growth and aging occur. A number of theories about the types of stress experienced by aging trees have been proposed (Ishii et al. 2007). Of the two studied in most detail, one is based on water relations (Ryan and Yoder 1997, Hubbard et al. 1999, Bond 2000, Hubbard et al. 2002, Woodruff et al. 2004), whereas the other is based on carbohydrate dynamics (Odum 1969, Grier and Logan 1977, Cannell 1989, Hunt et al. 1999). It would seem likely that more than one kind of stress is related to growth dynamics in old trees. There are also several ways in which old-growth trees can compensate for the stresses. In this work, we show how to integrate the multiple factors that are involved in aging and how both morphological and physiological characters may mitigate their effects, and we present a method of multi-criteria optimization that is new to tree physiology as a way of studying this complex of aging, morphology and physiology.



Figure 1. (a) Looking down on the canopies of *Abies* and *Pseudotsuga* at the Wind River Canopy Crane Research Facility (WRCCRF). *Abies* exhibits a more compact crown, and each group of foliage represents a separate branch from the trunk. *Pseudotsuga* exhibits waves of reiteration that places foliage throughout the width of the crown, and groups of foliage (i.e., SCUs) originate from the same branch. Photograph taken in June when currently developing foliage has a light green–yellow color. (b) Close-in picture of a major shoot cluster unit (SCU) axis, showing the distinction between lateral growth (SCU lateral axis, Orders 2 and 3) and epicormic growth (photo taken by Matt Schroeder, WRCCRF). (c) Accumulation of generations on a *Pseudotsuga* SCU. Black arrows point to a succession of new epicormic axes proliferating on top of the major axis of the parent SCU, with generations assigned assuming the parent SCU is Generation 1 (numbers in boxes).

Pseudotsuga menziesii (Mirb.) Franco (Douglas-fir), hereafter *Pseudotsuga*, is dominant in *Tsuga-Pseudotsuga* forests of the Pacific Northwest (Franklin and Dyrness 1973). Individual trees of *Pseudotsuga* achieve great longevity (up to 1400 years; Herman and Lavender 1990) despite evident constraints in annual growth (Ishii et al. 2000, Ishii et al. 2003). (Ishii and Ford 2001, Ishii and Ford 2002) propose that the persistence of *Pseudotsuga* depends on its capacity for continuous foliage production within its crown through the reiteration of existing branch structures (delayed adaptive reiteration, DAR; Figure 1). This is an expression of its morphology that is distinct from younger trees as well as from other species (Ishii and McDowell 2002). Understanding the importance of this growth form in the context of factors that may constrain net growth is complicated by the clear diversity of plant forms that coexist in old-growth forests of the Pacific Northwest. For example, both *Thuja plicata* Donn ex D. Don and *Abies amabilis* Dougl. ex Forbes inhabit the same forest type as *Pseudotsuga* and may live to the same or even more advanced ages (Minore 1990, Van Pelt 2001), although *Abies* tends to be shorter lived than *Pseudotsuga* and *Thuja*. These three (*Pseudotsuga*, *Thuja* and *Abies*) exhibit contrasting morphologies, yet they coexist in the same old-growth canopy; none of them can be considered to be exclusively 'optimal' relative to the others. We require a method whereby the performances of varying plant morphologies can be measured against multiple stresses that impact growth.

Functional-structural models

Kennedy et al. (2004) produced a functional-structural model (FSM) to simulate branch development in old-growth *Pseudotsuga* and to evaluate the effect of reiteration on long-term growth. In FSMs, biological processes are coupled with spatial representation of ideal plant form (Sievanen et al. 2000, Godin and Sinoquet 2005), which are then evaluated for the consequences of hypothesized responses of plant form

to internal and external conditions (Honda 1971, Fruh 1997, Reffye et al. 1997, Fournier and Andrieu 1999, Kaitaniemi et al. 2000, Percy et al. 2005, Sterck et al. 2005, Sterck and Schieving 2007). FSMs have promise to provide insight for the relationship between plant form and function, but for this promise to be fulfilled the models must be tested against processes that occur in real plants. Kennedy et al. (2004) demonstrate that reiteration has the potential to increase the longevity of a *Pseudotsuga* branch relative to a branch without reiteration, but their model is limited in its capacity to explain 'why' reiteration enables *Pseudotsuga* to overcome size-related constraints. Such an explanation requires relating alternative morphologies and processes of morphogenesis to the performance of the branch with respect to the many tasks involved in sustaining growth and then comparing those alternative morphologies to observed growth patterns.

A frequent technique to evaluate plant form and function (or organism behavior and function in general) is to apply an optimality argument, and simulation models are often used as optimization tools (Smith 1978). In the case of FSMs, the model is used to find the plant structure that performs best with respect to a measure of plant performance (e.g., light interception). It is rare that the actual plant structure matches the structure found to be optimal for a single measure (Honda and Fisher 1978, Honda and Fisher 1979, Farnsworth and Niklas 1995, Percy et al. 2005). Wright (1932), and again in 1988 (Wright 1988), characterizes fitness landscapes that contain multiple adaptive peaks which correspond to optimal phenotypes, and Farnsworth and Niklas (1995) describe how the number of these peaks increases as the number of requirements also increases, whereas the heights of individual peaks decrease towards the mean height across the landscape such that there is no single global optimum. From engineering, we know that optimal performance for multiple functions can cause suboptimal performances with respect to a single function (Niklas 1999). The main function of a branch is sustained growth, and to accomplish that function the branch

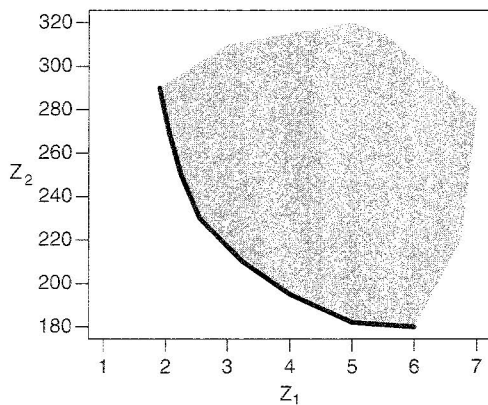


Figure 2. Consider a simulation model where parameter values are varied so that all possible combinations of two outputs, Z_1 and Z_2 , are produced (represented by the gray area). The optimization problem is to find the combinations of parameter values that minimize both criteria. Here we find that there is a trade-off between Z_1 and Z_2 , such that if there is an improvement in performance with respect to Z_1 (Z_1 gets lower), then performance with respect to Z_2 gets worse (Z_2 gets higher), and no single solution is able to minimize both simultaneously. Any solutions below the solid black line are not feasible given the model structure, and any solutions above the solid black line would be dominated by a solution along the solid line (performs worse with respect to both Z_1 and Z_2 relative to at least one solution along the solid line). The solid black line is called the Pareto optimal frontier and shows the set of mutually co-dominant solutions that are not dominated by any other solution.

structure must display foliage, transport materials and provide mechanical support; it is unlikely to be optimal for anyone of these tasks individually because it must contend with all simultaneously. We present a plant FSM of old-growth branch development that is optimized against multiple criteria using Pareto optimality. We use this approach to evaluate the relative importance of possible explanations for growth decline and to describe how morphology can affect the performance of a branch to compensate for stresses experienced with increases in size and age.

Pareto optimality

Pareto optimality allows for multiple criteria to be optimized simultaneously, and its central concept is nondominance (Figure 2). For example, suppose we want to compare the performance of two branches with respect to a vector of three criteria composed of a measure for hydraulics, a measure for foliage display and a measure for mechanical stability. If one branch performs better with respect to all three measures simultaneously, then it can be considered optimal relative to the other branch. However, if the first branch performs better with respect to hydraulics and mechanical stability, whereas the second branch performs better with respect to foliage display, then the two branches are mutually co-dominant—neither branch is exclusively optimal.

The FSM we use has parameters that, when varied, can produce a variety of branch morphologies that are only limited by those that can be accommodated by the underlying

structure of the simulation model (e.g., the feasible space in Figure 2). These morphologies may or may not correspond to the observed *Pseudotsuga* morphology. An evolutionary computation program (ECP; Reynolds and Ford 1999, Deb 2001) is used to search for sets of model parameters, each of which produces a unique branch morphology, that do best with respect to a number of requirements (the optimization criteria for the model). If a single solution is found that optimizes all criteria simultaneously, then the ECP will return that solution. However, if there are trade-offs among the criteria that prevent such a single optimal solution, then the ECP finds a set of multiple parameterizations (and thereby unique branch morphologies), such that each parameterization performs better with respect to a particular combination of assessment criteria than other members of the set. This set is called the nondominated Pareto frontier, the set of mutually co-dominant solutions not dominated by any other solution. Two criteria vectors are considered to be mutually co-dominant if improved performance with respect to one criterion comes at the expense of another criterion (Figure 2; Cohon 1978, p. 70; Appendix A, see Supplementary data).

Pareto optimality is a powerful tool for optimization problems with multiple criteria particularly when there are trade-offs among the criteria (Vrugt et al. 2007). A common technique when faced with multiple criteria is to combine the criteria into a single value through a scalar-valued function such as a weighted sum (Kim and Smith 2005). The weight assigned to each criterion measures its relative importance or serves to convert the multiple criteria to a single currency. There are many problems with the weighted sum technique (Kennedy et al. 2008). First, the approach assumes there is a well-defined global optimal solution and that, by minimizing the weighted sum, that solution can be found. Second, even if there is a single optimal solution, the approach requires a priori assignment of the relative importance of each of the multiple criteria to the single measure of performance in the optimization problem. The relative importance of a criterion to the performance of a branch is likely to vary both for a species as it ages and across varying environments as well as among species that co-occur in a common habitat. Furthermore, Farnsworth and Niklas (1995) describe the difficulty in converting multiple criteria to a single currency to optimize. They suggest multi-criteria optimization with Pareto optimality as an example of a technique that aids the optimization of multiple criteria against a set of unrelated currencies, which is preferable to the urge to 'shoe-horn multiple currencies into one for a cost-benefit analysis which does not fully capture the meaning of the different objectives.' Pareto optimality originated with the concept of utility in economics (Cirillo 1979) and is widely used in engineering and design (Statnikov and Matusov 1995). It has only more recently been applied to complex problems in biology and ecology (Rothley et al. 1997, Reynolds and Ford 1999, Turley 2001, Komuro et al. 2006, Vrugt et al. 2007, Kennedy et al. 2008, Turley and Ford 2009) and recommended as a tool to explain variability in optimal behavior (Schmitz et al. 1998).

A feature of Pareto optimality that is valuable for the study of complex biological questions is that it provides a discovery process for uncovering the relationships between the structure and functioning among species in a particular environment. The Pareto optimal frontier that we calculate is relevant to the system of interest insofar as the model produces branches that adequately replicate observed patterns. The intersection of the theoretical Pareto optimal space with the observed organism pattern shows the importance of this relationship relative to other possible structure--function relationships. If one accepts that in order to sustain growth a branch must perform many tasks, some of which may have conflicting requirements, then there are possibly multiple branch morphologies that balance those tasks with some success. These morphologies would depend on the relative importance of each of the tasks in a given environment and on the interaction between the morphology of a species and its physiology. The Pareto optimal frontier allows for a visualization of these solutions, where each point in the frontier corresponds to a unique branch morphology that is able to achieve a non dominated combination of criteria values. Vrugt et al. (2007) explain that for a multi-criteria function $F(0)$: 'The Pareto set of solutions defines the minimum uncertainty (variability) that can be achieved without stating a subjective relative preference for maximizing one specific component of $F(0)$ at the expense of another.' We find the solutions in the frontier that correspond to observed morphologies and contrast them to evaluate how the varying performances are achieved. This optimization is a first step that enables us to assess whether the simulated Pareto optima] frontier adequately characterizes processes in old-growth canopies. The simulation exercise then provides a path for future empirical research that can improve the modeling effort, whereby the performance of actual branches are measured for the criteria found to be important in the optimization process and interpreted in the context of their varying life history, physiology and morphology.

Methods

Pseudotsuga branch morphology

Ishii and Ford (2001) demonstrated that the foliage within *Pseudotsuga* crowns is regenerated through delayed adaptive reiteration (DAR), in which a reserve of buds is maintained along branch axes; these are later released to form new foliated shoots (Figure 1B). The resulting shoots are epicormic, and they are distinguished from shoots generated through the usual growth sequence and from adventitious shoots. These epicormic shoots proliferate new foliage in a pattern that closely resembles the architectural hierarchy exhibited by the branch (Figure 1). This hierarchy is described by a dominant Order 1 main axis with two to three daughter shoots per year and limited bifurcation on immediate lateral axes (Orders 2 and 3). The reiteration of this pattern is likely controlled via the establishment of apical control as the new epicormic axis develops

(Kennedy et al. 2004, Kennedy and Ford 2009). When an epicormic shoot successfully proliferates to replicate the characteristic architectural hierarchy, it forms an independent cluster of foliage, the shoot cluster unit (SCU; Ishii and Ford 2001). Up to seven generations of reiteration can form, with each generation proliferating on top of the previous one (Figure 1C). Reiteration of complete branches also occurs from the tree hunk at the base of dead or dying branches, and these can produce a secondary crown within the shell of the first (Ishii and Wilson 2001, Ishii et al. 2002, Van Pelt and Sillett 2008).

BRANCHPRO3

The FSM we developed is the third version of an FSM first presented by Kennedy et al. (2004) and assessed and improved by Kennedy and Ford (2009). The model objective is to simulate morphogenesis in old-growth *Pseudotsuga*. BRANCHPRO3 is a stochastic model that simulates two major processes of branch development on a yearly time step: release of suppressed buds proximally along major branch axes and the bifurcation of active terminal nodes (Figure 3). The combination of bud release and bifurcation determines the overall process of morphogenesis and the resulting branch morphology. Although we have elements for a theory for what influences bud release and bifurcation, each of these processes is still subject to unknown relationships and stochastic events. We therefore apply probability structures whose mean values relate to the possible influence of local variables on each process, but the realized value of each process is subject to stochastic influences. Details of the model structure and mathematical equations are provided in Appendix B (see Supplementary data). The simulated branch is initialized with a single foliated shoot, and branch development is simulated through 90 years.

There is a single suppressed bud for every Order 1 shoot. Every year, for every suppressed bud, the probability of release is calculated from Eq. (1) and the bud release tested against that probability (random number generators found in Press et al. 1999, pp. 282, 287, 294). If the bud is released, then it forms a new epicormic foliated shoot (e.g., Figure 1B). The second major model process is bifurcation. The bifurcation rate (r) is calculated (Eq. 2) for every foliated shoot with active buds (i.e., the current year's growth; Figure 3). If the computed value is <0 , it is given a value of 0. A random number is then drawn from a Poisson distribution, whose rate parameter is the function value r . If the random value drawn is >3 , then the number of daughter shoots assigned is exactly 3 (Appendix B). In BRANCHPRO3, a shoot retains its foliage for no more than 10 simulated years (Kennedy 2002, Kennedy et al. 2004), after which the shoot is not included in the population of foliated shoots. Individual clusters of foliage on the branch are tested each simulation year for whether they constitute an independent SCU. Shoot cluster units are assumed to only form on epicormic axes, and a cluster of foliage is considered independent of its parent SCU if its main axis continues to proliferate new foliage beyond 10 years. At the

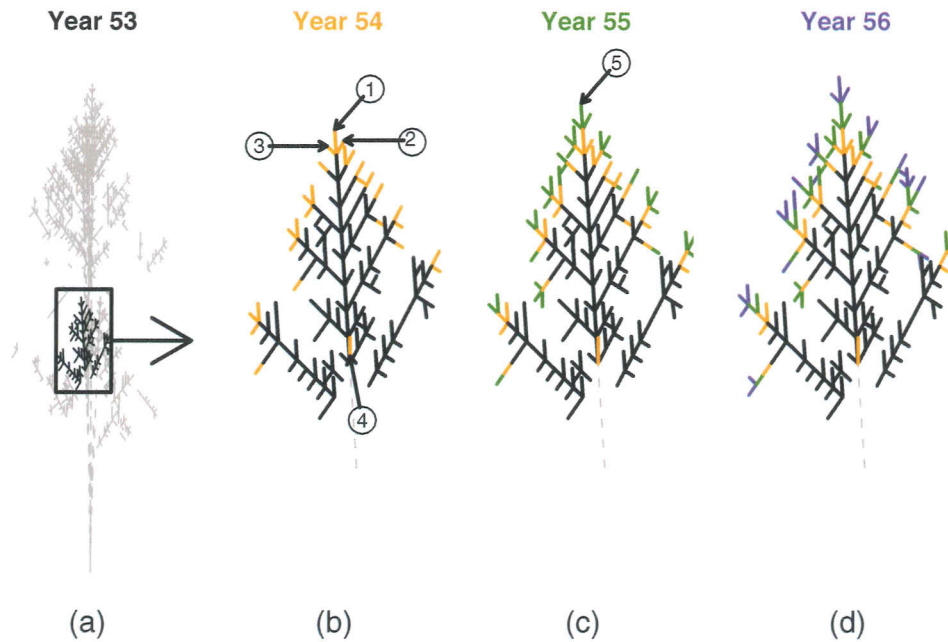


Figure 3. Sequence of yearly events during a simulation run of BRANCHPRO3. (a) 53 years simulated branch, with the SCU of interest highlighted (black). Dashed gray lines are Order 1 shoots that have lost their foliage, remaining lines are foliated shoots on the branch. (b) close-in view of SCU at 54 years, with new shoots in orange. The production of new shoots is a random process, whose rate depends on the conditions of the neighboring shoots (Eq. 2). Note that Shoot 4 is a new epicormic shoot produced from a bud release from suppression at that point. All Order 1 main axis shoots (with and without foliage) contain suppressed buds that are tested once each year for release (Eq. 1). (c) SCU at 55 years, with new shoots in green. Note that Shoot 2 (an Order 2 lateral axis) failed to produce new shoots the next year, whereas Shoots 1 (Order 1 main axis) and 3 (Order 2 lateral axis) each produced three new shoots. Shoot 4 (new epicormic) failed to produce a new shoot and therefore will not produce a new SCU. All of the remaining suppressed buds failed tests of release and will be tested again the next time step. (d) SCU at 56 years, with new shoots in blue. Shoot 5 (Order 1 main axis) produced three new shoots, whereas the immediate lateral axes both failed to produce new shoots.

end of the simulation, values are calculated that evaluate the performance of the branch relative to a set of design criteria (described below). The components of the model that are evaluated in the optimization are the variables and parameters associated with each of the two major model processes, bud release from suppression (Eq. 1) and bifurcation (Eq. 2).

BRANCHPRO3: bud release from suppression and bifurcation

We developed functions that relate the values of bifurcation (r) and bud release from suppression (P) to a set of independent variables (Table 1; Kennedy 2008), with nonlinear monotonic relationships (see Appendix B for details). The constants k_{2j} relate to the shape of those relationships, and the functions were assessed by Kennedy (2008).

$$p(t_{\text{bud}}, a, d_{\text{SCU}}, d_{\text{stem}}) = p_0 + p_{\text{bud}} \left(\frac{t_{\text{bud}}}{k_{21} + t_{\text{bud}}} \right) + p_a * a + p_{\text{SCU}} \left(\frac{d_{\text{SCU}}}{k_{22} + d_{\text{SCU}}} \right) + p_{\text{stem}} \left(1 - \frac{d_{\text{stem}}}{k_{23} + d_{\text{stem}}} \right), \quad (1)$$

$$r(o, g, n_{\text{over}}, t_{\text{base}}, d_{\text{base}}) = r_0 + r_{\text{ord}} \left(1 - \frac{1}{o} \right) + \frac{r_{\text{gen}}}{d_{\text{base}}} \left(\frac{g}{k_{24} + g} \right) + r_{\text{over}} \left(\frac{n_{\text{over}}}{k_{25} + n_{\text{over}}} \right) + \frac{r_{\text{base}}}{d_{\text{base}}} \left(\frac{t_{\text{base}}}{k_{26} + t_{\text{base}}} \right) \quad (2)$$

The functions are updated each year for each shoot as the values for the independent variables change. The magnitude and direction (increasing or decreasing) of each component of the function that corresponds to a single independent variable (e.g., the bud age t_{bud}) are controlled by the value of the parameter associated with it (e.g., P_{bud}). As in a simple multiple regression model, a parameter value of 0 can be interpreted to mean that the corresponding independent variable does not change the computed value of the function. A positive parameter value means that the function value increases with the corresponding function component, and a negative value means the function value decreases with the corresponding function component. Each function also has

Table 1. Independent variables, associated parameters and underlying process assumptions in BRANCHPRO3. The parameters determine the direction (positive or negative, i.e., decrease or increase function value with increasing independent variable) and the magnitude (i.e., the size of the effect of increasing the independent variable on the function value) of the associated independent variable on the function value for each process (bud release from suppression (p) and bifurcation (r)).

Variable	Parameter	Description	Process assumption
p function	p_0	Baseline probability	If all other parameters or variables are zero, this is the probability of release. The effects of the variables are measured against this baseline
t_{bud}	p_{bud}	Age of bud	The probability a bud is released is related to its time since suppression
a	p_a	Proportion of inactive axes	The inhibition of the bud declines as neighboring growth slows, measured by the proportion of axes immediate to the current bud (main axis, lateral axes immediately subtended on either side of the bud) no longer proliferating
d_{SCU}	p_{SCU}	Distance to the nearest SCU on the same axis	The active growth of higher generation foliage along the same main axis inhibits bud release, and this effect is stronger the closer the growth is to the current bud
d_{stem}	p_{stem}	Distance to main stem	Hydraulic status lessens with distance to the base of the main branch stem
r function	r_0	Baseline bifurcation	If all other parameters or variables are 0 (or 1 for order), this is the rate of bifurcation. The effects of the variables are measured against this baseline
o	r_{ord}	Shoot order	Apical control regulates bifurcation by shoot order. In the process of reiteration apical control is established; the main stem of SCUs are considered Order 1
g	r_{gen}	Shoot generation	A severe hydraulic constriction occurs at a junction formed by bud release from suppression, and this constriction worsens for each new generation
n_{over}	r_{over}	Number of overlapping foliated shoots	Foliage display is approximated by a count of the number of foliated shoots of the same generation or higher that intersect with the current shoot
t_{base}	r_{base}	Bud age at SCU base when it was released from suppression	A severe hydraulic constriction occurs at a junction formed by bud release from suppression, and this constriction worsens the longer the bud is suppressed before it is released
d_{base}	none	Distance to SCU base	The hydraulic constriction caused by the junction formed by bud release from suppression lessens with distance along the main axis to the base of the axis

an intercept (P_0, r_0) that provides a baseline function value that is not related to any independent variable. The value of bifurcation is calculated for each foliated shoot with active meristems, and the value of probability of bud release from suppression is calculated each simulation year for each suppressed bud. The independent variables represent possible biological features that may affect the value of either bifurcation or bud release from suppression.

In BRANCHPRO3, the probability that a suppressed bud is released may depend on the bud age as measured by the number of years since the bud was fanned (t_{bud} ; Bryan and Lanner 1981, Ishii and Ford 2001, Kennedy et al. 2004), on the activity of neighboring axes as measured by the proportion of immediate axes still actively proliferating foliage (a) and on the proximity of other active foliage clusters as measured by the distance to the nearest SCU along the same axis

(d_{SCU}). The variables a and d_{SCU} represent the correlation of epicormic initiation with a slowing of growth, often explained by a hormonal effect (Bachelard 1969, Kormanik and Brown 1969, Remphrey and Davidson 1992, Nicolini et al. 2001, Nicolini et al. 2003). The potential hydraulic status of a bud (Wignall et al. 1987) is represented by the proximity of the bud to the main stem as measured by the distance (centimeters) between the bud and the main stem (d_{stem}). The closer the bud is to the main stem, the higher the probability that it is released (Eq. 1).

In BRANCHPRO3, we do not incorporate resource dynamics directly into the production of new shoots; rather, we relate bifurcation to variables associated with resource capture and to the internal controls on foliage production. We evaluate how the rate of bifurcation (r ; Eq. 2) changes with architectural status (o , shoot order determined by architectural hierarchy, with order increasing at each lateral junction and new epicormic shoots assigned Order 1) and for new epicormic shoots with increasing generation (g ; Kennedy et al. 2004). There may be a more severe hydraulic constriction at junctions formed by epicormic bud sprouting than junctions formed by sequential lateral growth (Schulte and Brooks 2003, Kennedy 2008), and the severity of the junction constriction may change with the age of the bud that was released when it formed that axis (t_{base}). This hydraulic constriction may lessen as the axis extends beyond the junction (Tyree and Ewers 1991), represented by the distance from the base of the SCU (d_{base} ; Appendix B). Finally, bifurcation is also proposed to change with within-branch foliage overlap (n_{over}). The magnitude and direction of each of these effects on bifurcation are determined by the values of the parameter corresponding to each independent variable.

Figure 3 illustrates the progression of growth for an SCU in BRANCHPRO3. Each year, for each new shoot the value of r is calculated based on the parameter values for that simulation and the values of the independent variables for that

Table 2. Optimization criteria. Target ranges are set for each of the empirical criteria (taken from Ishii and Ford 2001), whereas the design criteria are minimized. R_b defines the mean number of foliated shoots for a given shoot order (Orders 1, 2 and 3) on a simulated branch. The design criteria are the mean number of cumulative junctions ($\mu_{\text{junctions}}$), the mean path length from the base of the branch to active terminal shoots (μ_{path}), the relative mechanical requirements for a given distribution of foliage (load) and the mean number of overlapping foliated shoots (μ_{over}).

Name	Type	Target	Value
n_{foliated}	Empirical	[2500,6500]	Number of foliated shoots
n_{SCUs}	Empirical	[20,50]	Number of foliated SCUs
length	Empirical	[240,430]	branch length (cm)
arch_mod	Empirical	1	1: ($R_{b1} > R_{b2} > R_{b3}$) 0: otherwise
$\mu_{\text{junctions}}$	Design	Minimize	$\frac{1}{n_{\text{term}}} \sum_{i=1}^{n_{\text{term}}} n_{\text{turns}}(i)$
μ_{path}	Design	Minimize	$\frac{1}{n_{\text{term}}} \sum_{i=1}^{n_{\text{term}}} l_{\text{path}}(i)$
load	Design	Minimize	$\sqrt[4]{\frac{P_{1/2}}{8P_1}} + \sqrt[4]{\frac{P_{2/3}}{27P_1}}$
μ_{over}	Design	Minimize	$\frac{1}{n_{\text{foliated}}} \sum_{i=1}^{n_{\text{foliated}}} n_{\text{over}}(i)$

shoot in that year. From the value of r , a random value from the Poisson distribution is drawn to determine the number of daughter shoots to be produced the next year. Suppressed buds are found along Order 1 axes, and each year for each suppressed bud, the probability of release is calculated based on the parameter values for that simulation and the values of the independent variables for that bud in that year. The bud is then tested for release against that probability, and if it succeeds it forms a new epicormic shoot. The value of r for the new epicormic shoot is calculated, and this is used to determine the number of daughter shoots to be formed from it the next simulation year. The model structure as we describe it constrains the possible morphologies that can be simulated in the optimization search and thereby defines the feasible space in Figure 2. The rules for foliage proliferation ensure that simulated branch structures are consistent with observed growth regulations in the old-growth branches. The values of the multiple criteria are calculated for a branch after 90 years of branch development, which is near the mean age of six of the nine branches sampled by Ishii and Ford (2001).

Multi-criteria optimization

The multi-criteria optimization includes both empirical and design criteria (Table 2). The empirical criteria are included to evaluate whether the solutions that are Pareto optimal with respect to the design criteria also match the observed *Pseudotsuga* branch pattern. The four design criteria define possible constraints for which an old-growth branch may compensate. The optimization procedure is conducted by simulating many unique combinations of values for the ten parameters (*e.g.*, p_0 , p_{bud} , r_{over} , r_{base}). These parameters determine the relative effects of each of the independent variables on the two major processes (p and r) and result in varying patterns of morphogenesis and in unique branch morphologies. Each simulated

branch is then used to calculate the optimization criteria and evaluated for its performance relative to other simulated branches. The focus of the optimization is the process of morphogenesis and the resulting branch morphology, and we do not explicitly include a resource constraint in the optimization. The solutions available to the optimization are constrained by the underlying model structure, which was designed to mimic the developmental pathways observed in *Pseudotsuga*. Optimization results must be interpreted in the context of the FSM process structure and its relationship to our understanding of the observed processes. The parameter search is conducted using an evolutionary algorithm that had been previously developed for ecological models (Reynolds and Ford 1999).

Empirical criteria

The empirical criteria are designed to capture the basic branching pattern of old-growth *Pseudotsuga* and to constrain a portion of the optimal set to be consistent with the observed *Pseudotsuga* architectural pattern. This ensures that, without explicit consideration of resource dynamics, the level of foliage production is commensurate with that achieved by *Pseudotsuga*.

Targets for the empirical criteria are based on the empirical work of Ishii and Ford (2001) at the Wind River Canopy Crane Research Facility (WRCCRF; trees were ~400 years old; Shaw et al. 2004). Six of the branches they sampled were near 90 years old, and the remaining three were near 145 years old. We used values they measured for the 90-year branches to set the upper and lower limits for the empirical target ranges of the first three empirical criteria (Table 2), because that branch year is represented by more individuals in the observed set of branches, and for computational efficiency. Results calculated for 145-year branches are consistent

with the results presented here (Kennedy 2008). The empirical criteria are the number of foliated shoots at 90 years (nfoliated), the number of independent SCUs with foliated shoots at 90 years (nSCUs) and the length of the branch at 90 years (length). The fourth empirical measure (arch.rnod) evaluates whether the branch follows the characteristic architectural hierarchy of *Pseudotsuga*. It is given a value of 1 if the branch follows the observed hierarchy (Order 1 bifurcation greater than Order 2 bifurcation, which is greater than Order 3 bifurcation), a 0 otherwise. Any simulated branch that is able to achieve values within the target range for all four of these empirical criteria simultaneously is assumed to adequately replicate the observed branch pattern.

Design criteria

The four design criteria relate to two major theories proposed to explain the frequent observation that tree growth declines with increasing tree size (Gower et al. 1996, Mencuccini and Grace 1996, Ryan et al. 1997, Ryan and Yoder 1997, Bond 2000, Acker et al. 2002, Ryan et al. 2004). A recent theory proposes that growth decline is caused by hydraulic limitation (Bond 2000), whereas an older theory is that, with increase in tree size, there is an increase in the demands of the tree for carbohydrate relative to a given level of production (Odum 1969, Grier and Logan 1977, Cannell 1989, Hunt et al. 1999). There is evidence of several processes in *Pseudotsuga* that compensate for growth limitations via physiological and structural changes that mitigate the effects of size on net production (McDowell et al. 2002b), mostly evaluated with respect to hydraulic limitation; these include changes in leaf water potential and foliar osmotic potential, changes in the leaf area to sapwood area ratio (LA:SA; McDowell et al. 2002a, 2002b, Barnard and Ryan 2003, Woodruff et al. 2004), changes in sapwood hydraulic conductivity and storage (Phillips et al. 2003, Cermak et al. 2007) and hydraulic lift by both horizontal and vertical roots (Warren et al. 2007). In general, however, these studies do not consider whether the morphology (or growth pattern) of old-growth trees may also compensate for size-related constraints. For the purpose of the branch optimization, we focus on the potential for morphology to reduce hydraulic limitation and increase the photosynthesis:respiration ratio (thereby reduce carbon limitation).

Hydraulic constraints

The first two design criteria measure the impact on morphology for two possible hydraulic constraints. The resistance of water flow to a particular foliage cluster in the crown is a function of path length from the soil to the leaf, specific conductivity of the wood sections along this pathway, the possible restrictions associated with branching points and xylem area that can supply water to the foliage (Zimmermann 1978, Tyree and Zimmermann 2002). Quantifying all of these components requires a highly detailed model, which is out of the scope of the current modeling effort. We focus on the possible hydraulic restriction

associated with branching points (Larson and Isebrands 1978, Zimmermann 1978, Ewers and Zimmermann 1984a, 1984b, Tyree and Alexander 1993) and on the effect of increasing resistance with increasing path and branch length (Tyree and Ewers 1991, Waring and Silvester 1994, Panek and Waring 1995, Walcroft et al. 1996). A branch morphology with a smaller number of cumulative junctions from its base to the terminal foliage may perform better than a branch with a higher number of cumulative junctions. Furthermore, a branch with a shorter path length for water transport from the base of the branch to terminal foliage may perform better than a branch with a longer path length. A branch with smaller values of both the number of cumulative junctions and path length may perform better than one with higher values of either variable. The mean number of junctions to terminal foliage ($U_{\text{junctions}}$) and the mean path length to terminal foliage (U_{path}) are the first two design criteria included in the multi-criteria optimization (Table 2).

Carbon limitation

The third and fourth design criteria evaluate the possible role of morphology in increasing the ratio of photosynthesis to carbohydrate requirement. Ishii et al. (2007) state that the increase of productive tissue relative to nonproductive tissue is one way in which DAR may decrease the respiration to photosynthesis ratio. Because DAR arises from main branch axes, it concentrates mechanical stress produced by new foliage toward the stem where foliage has already been supported, relative to that for non-reiterating branch expansion. This lessens the requirement for support tissue. A morphology that decreases diameter requirement distally on the branch (at one-half and two-thirds branch length; $P_{1/2}$; $P_{2/3}$) relative to the base (P_1) would decrease new wood growth requirement relative to a given level of photosynthesis (load; Table 2). The value of load is calculated as the sum of the ratios of diameter required at one-half and two-thirds the branch length, relative to the base of the branch (adapted from Percy et al. 2005, Morgan and Cannell 1988, Cannell 1989). If all of the foliage is displayed at the terminal end of the branch, then this ratio takes a maximum value of 1.034 (Appendix B; Table B2). This criterion is reduced as the foliage is displayed more evenly along the major branch axis. Another way the ratio of photosynthesis to respiration may increase relative to a given carbohydrate demand would be a morphology that more effectively displays foliage to light, relative to other morphologies, through the production of epicormic axes (Ishii et al. 2007). *Pseudotsuga* is generally considered a shade intolerant species with a sparse crown (Minore 1979), so it is important for foliage in *Pseudotsuga* to be displayed in a manner that increases light interception. Ishii et al. (2007) hypothesize that DAR may place shoots in better illuminated areas within the crown. For the final design criterion, we calculate the number of foliated shoots overlapping each other foliated shoot on the branch and average that across all foliated shoots (U_{over}) If the foliage is displayed

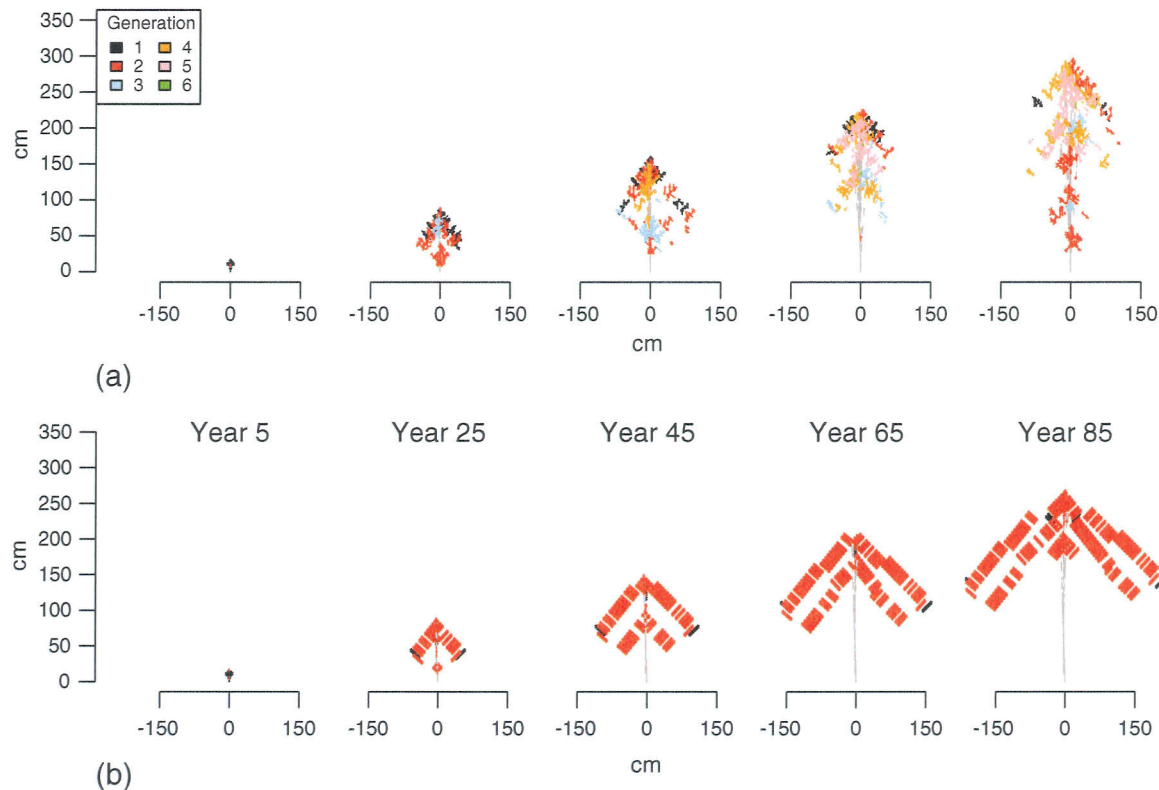


Figure 4. Examples of branch development over time for a branch (a) characteristic of the set that tends to minimize the mean path length from the branch stem to terminal active foliage (Low_{path}) and a branch (b) characteristic of the set that tends to minimize the mean number of cumulative junctions to terminal foliage ($Low_{junctions}$). Branches progress from Yr5 to Yr25, Yr45, Yr65 then to Yr85. The morphology exhibited by each at Yr85 clearly differs. The branch forms are similar early in development then diverge with respect to the degree of reiteration and the accumulation of higher generation foliage. We can visually see how branches in Low_{path} tend to decrease mean path length (μ_{path}) relative to branches in $Low_{junctions}$ and how branches in $Low_{junctions}$ tend to have lower mean number of cumulative junctions to terminal foliage ($\mu_{junctions}$).

efficiently, then the value of μ_{over} would be smaller than for a branch that displays its foliage less efficiently.

Results

The Pareto optimal set contains all combinations of parameter values that yield Pareto optimal criteria results or the parameter combinations that correspond to the solid line in Figure 2. Pareto optimal solution sets are complex because they contain many dimensions of both parameters and criteria. Useful summaries of these are key to understanding the results, and Kennedy et al. (2008) recommend performing a post hoc partition of the solution space that allows for an efficient contrast among larger groups of solutions. Kennedy (2008) found trends in the minimum values of the design criteria with changing parameter values (Appendix C, see Supplementary data) and from those trends established meaningful partitions of the Pareto optimal space for BRANCHPRO3. In particular, clusters of parameterizations were able to achieve minimum values of some design criteria that were not achieved by

other clusters of parameterizations (Appendix C). We compare the two partitions with respect to several measures, including the criteria performance and the morphological characteristics of each.

Pareto optimal solution set: criteria performance

Simulated branches in the Pareto optimal solution set exhibit a range of morphologies, with distinct morphological patterns at either end of the range (Figure 4). These two morphological types correspond both to distinct clusters of parameterizations in the Pareto optimal solution set as well as to varying performance with respect to the design criteria (see Appendix C). The trends in the minimum value achieved with respect to the design criteria show that clusters of parameter values able to achieve minimum values of $\mu_{junctions}$ are unable to also achieve minimum values of μ_{path} . There is no such strong partitioning of the parameter space for load and μ_{over} such that minimum values of these two criteria are achieved across the combinations of parameter values (Appendix C). Due to the clear distinction in the relative performance of the two

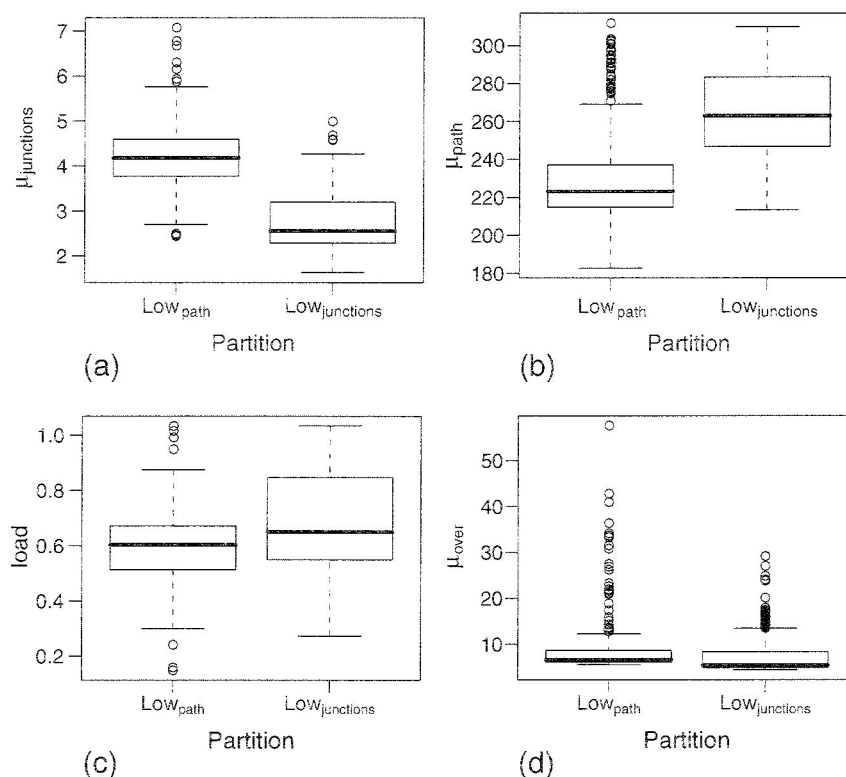


Figure 5. (a) The distribution of values for the mean number of cumulative junctions to terminal foliage ($\mu_{junctions}$) is shifted higher for Low_{path} relative to $Low_{junctions}$, indicating that $Low_{junctions}$ tends to perform better with respect to $\mu_{junctions}$. Low_{path} is unable to achieve the minimum value of $\mu_{junctions}$. (b) The distribution of values for mean path length to terminal foliage (μ_{path}) is shifted lower for Low_{path} relative to $Low_{junctions}$, indicating that solutions in Low_{path} tend to perform better with respect to μ_{path} , and solutions in $Low_{junctions}$ are unable to achieve the minimum value of μ_{path} . (c) Solutions in Low_{path} tend to perform similarly with respect to relative mechanical requirements (load) compared to solutions in $Low_{junctions}$, although the distribution of values is shifted slightly lower for Low_{path} . This difference is much smaller than that for $\mu_{junctions}$ and μ_{path} . (d) The distributions of values of the mean number of overlapping foliated shoots (μ_{over}) are similar between Low_{path} and $Low_{junctions}$, although the distribution for $Low_{junctions}$ might be shifted slightly lower. This difference is much smaller than that for $\mu_{junctions}$ and μ_{path} .

groups of morphologies with respect to the two hydraulic criteria, we label the first partition $LOW_{junctions}$ and the second partition LOW_{path} (Figure 5). By partitioning the solution space in this manner, we are able to form an effective contrast by focusing on two clusters of solutions within the entire solution set. This is akin to comparing solutions that correspond to the lower right-hand portion of the line in Figure 2 to the solutions that correspond to the upper left hand portion. Since this is a 4D space, we also must consider the differences between the partitions in load and U_{over} . Values of load tend to be slightly higher in $LOW_{junctions}$ relative to LOW_{path} (Figure 5C) and U_{over} slightly lower in $LOW_{junctions}$ relative to LOW_{path} (Figure 5D), although the distinction in performance between the partitions is not dramatic with respect to these two criteria.

The two partitions of the parameter space are also clearly differentiated with respect to their tendency to satisfy the empirical criteria (Table 3). While both partitions are able to consistently satisfy the number of foliated shoots and branch length, a greater proportion of solutions in Low_{path} are able to satisfy both the number of SCUs and the characteristic archi-

tectural model of *Pseudotsuga* than solutions in $LOW_{junctions}$. This implies that branches in the LOW_{path} partition more closely match the observed *Pseudotsuga* branch pattern because they are able to achieve more of the empirical criteria. It also clearly demonstrates that multiple measures are required to evaluate whether a simulated branch morphology is able to adequately replicate the observed morphology. Furthermore, within each partition, there is variability in the number of SCUs that are produced on simulated branches. The number of SCUs is a measure of the level of reiteration that occurs throughout branch development, and branches in LOW_{path} exhibit more SCU development (and, hence, greater reiteration) than branches in $LOW_{junctions}$ (Table 3). By using the number of SCUs as a surrogate for the level of reiteration, we can evaluate how increasing reiteration modifies performance of a branch with respect to the design criteria. We fit linear models to the relationship between the number of SCUs and the value of each of the design criteria. If the value of a design criterion significantly decreases with the number of SCUs on the branch, then increasing reiteration improves

Table 3. Summary comparison of the two partitions in the Pareto optimal results (Low_{path} , $Low_{junctions}$). The percentage of empirical criteria satisfied within each group indicates how closely the set of solutions tend to replicate the observed *Pseudotsuga* branch pattern (higher % = better match). The percentage of solutions with the number of shoot cluster units (SCUs) below the target range indicates how many solutions have limited reiteration compared to *Pseudotsuga*. Median values of g^* for each partition, at zero n_{over} , compared to the maximum value observed in *Pseudotsuga*. Slope of linear relationship between design criteria and the number of shoot cluster units (SCUs). All linear slopes are significant at 0.05. Simulated bifurcation is the mean number of daughter shoots for a shoot of a given order on a simulated branch ($Rb1_{sim}$, $Rb2_{sim}$, $Rb3_{sim}$). Timing of bud release and proportion of SCUs still proliferating at 90 years, with a value above 1 suggesting no SCU turnover within 90 years.

		Low_{path}	$Low_{junctions}$
Percentage empirical criteria satisfied			
nfoliated		99%	96%
nSCUs		56%	17%
length		99%	99%
arch_mod		95%	68%
Percentage SCUs below target		41%	83%
Percentage SCUs above target		3%	0%
Slope of relationship with SCUs			
$\mu_{junctions}$		-0.017	0.05
μ_{path}		0.53	-1.4
load		0.0017	-0.01
μ_{over}		0.3	-0.027
Simulated bifurcation (Rb; median)	<i>Pseudotsuga</i>		
$Rb1_{sim}$ (Order 1)	2.5	2.72	2.88
$Rb2_{sim}$ (Order 2)	1.5	1.57	2.75
$Rb3_{sim}$ (Order 3)	0.5	0.57	0
SCU dynamics			
Maximum generation (g^* , median)	7	8.9	2.75
Timing of bud release (median)		6	5
Proportion SCUs still proliferating 90 years (median)		0.786	1.17

performance with respect to that criterion. If there is an opposite effect for another criterion, then increasing reiteration worsens performance with respect to that criterion.

Among solutions in the Low_{path} partition, $U_{junctions}$ significantly decreases with the number of SCUs: branches with more SCUs perform better with respect to $U_{junctions}$. The remaining design criteria significantly increase with the number of SCUs, such that branches with more seus perform worse with respect to U_{path} , load and U_{over} (Table 3). These relationships are for a set of simulated branches that already maintain some level of reiteration commensurable with that observed for *Pseudotsuga*, as the majority of solutions in this partition achieve numbers of seus within the observed range. This is explained by the manner in which foliage is distributed among seus on a simulated branch. We can compare two branches in the Low_{path} partition, with similar numbers of foliated shoots, but one branch has 15 SCUs and the other branch has 25 SCUs. In order for the first branch to achieve a comparable number of foliated shoots on fewer SCUs, more foliage must be produced on higher ordered lateral axes. In fact, within Low_{path} , as the number of seus increases, then the average simulated bifurcation of Orders 2 and 3 shoots decreases (Appendix C). For a given generation, this increases the number of junctions to foliated shoots. In contrast, a simulated branch with more seus would have fewer shoots on lateral axes, which decreases the mean number of cumu-

lative junctions. The trade-off is that, since basal reiteration is rare, the additional seus are likely to occur relatively distally on the major branch axis. This results in increased path lengths and relative mechanical requirements. In addition, reiteration occurs on the existing branch framework and within the tree crown. This is a limited space, such that within-branch foliage overlap would increase with the number of seus, making it more crowded within that established framework and increasing foliage overlap.

In contrast, among branches in the $Low_{junctions}$ partition, there is a pattern in the relationships between the design criteria and the number of seus that is opposite to that observed within the Low_{path} partition. In $Low_{junctions}$, $U_{junctions}$ increases with the number of seus, and the remaining criteria decrease (Table 3). Branches in $Low_{junctions}$ are characterized by low levels of reiteration (i.e., tend to have very few SCUs). The consequence of increasing the number of SCUs on a branch with very limited reiteration can be visualized with the help of Figure 4B, Year 85. If we assume that the number of foliated shoots on this branch is held constant, an increase in the number of seus would entail removing foliage from the extensive lateral axes of the branch and placing them in a new seu proximally along the major branch axis; this new seu would be of higher generation. This would clearly reduce the mean path length, relative mechanical requirement and the foliage overlap. If, however, the re-

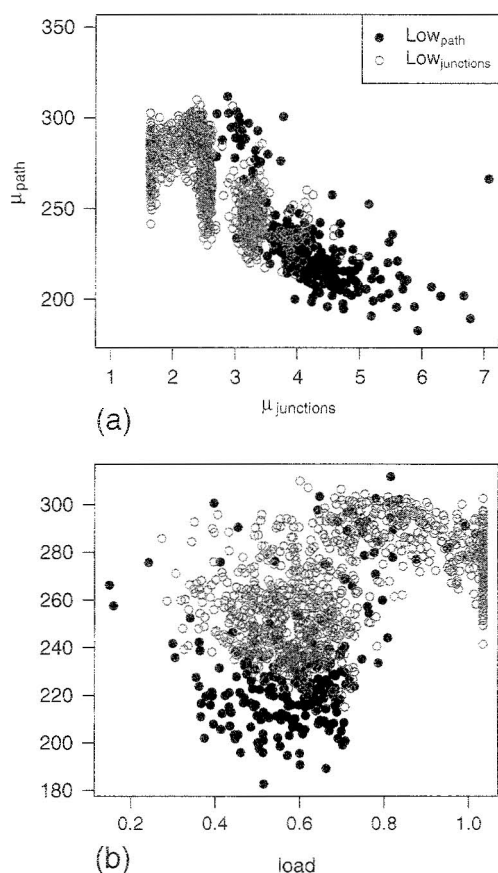


Figure 6. (a) There is a negative trade-off between the mean number of cumulative junctions to terminal foliage ($\mu_{\text{junctions}}$) and mean path length to terminal foliage (μ_{path}) for both LOW_{path} (filled) and $\text{LOW}_{\text{junctions}}$ (open), although the location of the curves differ. This relationship is similar to those observed for $\mu_{\text{junctions}}$ with both n_{over} and load (Appendix C). (b) Mean path length (μ_{path}) seems to increase with relative mechanical requirements (load). This relationship is qualitatively similar to those observed for all pair-wise combinations of design criteria that do not include $\mu_{\text{junctions}}$ (Appendix C).

iteration faithfully replicates the underlying architectural pattern, then this would increase the maximum number of junctions on this branch by 1; this increase is accounted for by the increase in generation. In essence, increasing the seus for a branch in $\text{LOW}_{\text{junctions}}$ puts that branch closer in morphology to branches in LOW_{path} , characterized by lower mean path length and higher number of junctions.

These relationships between the design criteria and increasing levels of reiteration demonstrate that the number of SCUs on a *Pseudotsuga* branch is influenced by the trade-offs among the design criteria, and these trade-offs are characterized mainly by the opposite trend between $\mu_{\text{junctions}}$ and the remaining design criteria. The trade-offs among the design criteria are clear in pair-wise scatter plots, where there are negative trends for $\mu_{\text{junctions}}$ with each of the other three design criteria (Figure 6; Appendix C).

Comparison of branch morphologies

The number of parameters in BRANCHPRO3 make it difficult to compare individual parameters and their effect on the Pareto optimal solution space (see Appendix C for distributions of parameter values). Instead, we evaluate how the integrative effects of a parameter vector within a given simulation modify the process of morphogenesis and the resulting branch morphologies.

Simulated bifurcation and timing of bud release

We calculate the mean number of daughter shoots for each shoot order on branches simulated from all solutions in each partition (Table 3). The mean number of daughter shoots on simulated branches for shoot Orders 1 (Rb1_{sim}), 2 (Rb2_{sim}) and 3 (Rb3_{sim}) are similar between the LOW_{path} branches and the observed *Pseudotsuga* pattern, whereas the mean number of daughter shoots for Orders 2 and 3 shoots for branches simulated in the $\text{LOW}_{\text{junctions}}$ partition clearly differ from *Pseudotsuga* and violate the architectural hierarchy as defined by arch_mod . This pattern of bifurcation interacts with the timing of bud release to influence the production of seus.

The median value of timing of bud release for branches simulated in the LOW_{path} partition is significantly greater than the median timing in $\text{LOW}_{\text{junctions}}$ (Wilcoxon rank-sum test, $P < 0.05$), i.e., buds are suppressed longer before they are released, and regeneration of foliage occurs more proximally along major branch axes in LOW_{path} than in $\text{LOW}_{\text{junctions}}$ (Table 3). The dynamics of the population of SCUs on the branch also differs between the two partitions. We consider the ratio of actively proliferating SCUs at 90 years relative to the number of new SCUs (Generation 2 or higher) produced throughout the branch lifespan; a value of 1 or above would indicate that all SCUs that ever emerged on the branch are still actively proliferating at the end of the simulation, and a value below 1 indicates that some of the SCUs failed to produce foliage and are terminated before the end of the simulation (SCUs turnover). The distribution of this proportion was shifted below 1 for solutions in LOW_{path} and above 1 for solutions in $\text{LOW}_{\text{junctions}}$ (Table 3). This indicates that SCUs on branches simulated in LOW_{path} proliferate for some time then decline. This pattern is consistent with the stages of seu development described by Ishii and Ford (2001) and is explained by the lower values of mean bifurcation on simulated branches for LOW_{path} compared to $\text{LOW}_{\text{junctions}}$. In contrast, in $\text{LOW}_{\text{junctions}}$ if an seu develops on the branch it persists throughout the branch lifespan (Table 3) with both primary and secondary axes enduring. These results indicate that buds are released earlier on $\text{LOW}_{\text{junctions}}$ branches relative to LOW_{path} , and once a new SCU is established for $\text{LOW}_{\text{junctions}}$ it continues to proliferate throughout the branch lifespan.

Generation threshold and expected bifurcation

The value of r (bifurcation rate) is calculated from the combination of independent variables and parameter values (Eq.

2). When the parameter values are negative, then r decreases with increasing independent variables. This means it is possible that, at some value of the independent variables, the calculated value of r will be zero; when r is zero, that shoot will fail to produce daughters. A threshold value for bifurcation as the value of an independent variable at which the value of r is 0 can thereby be calculated (Appendix B). In particular, if r decreases with increasing generation (g ; a new generation forms at each bud release from suppression; Figure 1C), then we can calculate the generation at which a new epicormic shoot will no longer proliferate. This is also the maximum generation at which a new SCU can develop (which we label g^*). We evaluate how the maximum SCU generation changes with increasing overlap of the new epicormic shoot by calculating g^* for new epicormic shoots with increasing n_{over} .

The value of g^* tends to be higher in LOW_{path} than in $\text{LOW}_{\text{junctions}}$ across all values of n_{over} (Table 3; Figure 7), such that it is possible for new epicormic shoots to proliferate at higher generations in LOW_{path} . The value of g^* tends to decline more sharply with n_{over} for LOW_{path} than $\text{LOW}_{\text{junctions}}$. This pattern shows the interaction between bud release from suppression and the bifurcation of new epicormic shoots in the process of DAR that is prevalent in LOW_{path} branches. Whether a new epicormic shoot that is released from suppression successfully proliferates depends both on its generation as well as on the presence of surrounding foliage. For example, in LOW_{path} , a Generation 4 new epicormic shoot may still proliferate even if it is overlapped by five or fewer shoots. This enables a lower-generation new epicormic shoot to emerge from an area of moderate overlap and possibly proliferate into an area of lower overlap (as further proliferation is also mitigated by foliage overlap, see below). In contrast, a Generation 7 new epicormic shoot will fail to proliferate if even one other shoot overlaps it, and in general no Generation 8 new epicormic shoot can proliferate. This implies that, as the generation of a new epicormic shoot increases, it is more difficult for that shoot to successfully proliferate, and higher generation shoots cannot tolerate higher foliage overlap and still proliferate. In contrast, a $\text{LOW}_{\text{junctions}}$ branch will not proliferate foliage of higher generation (e.g., > 4) regardless of the presence of surrounding foliage.

We also calculate the expected number of daughter shoots ($E(k)$) for any shoot with specified values of the independent variables (Appendix B). For both partitions, this number declines with increasing n_{over} which implies that foliage overlap mitigates the production of new foliage. If a shoot finds itself in an area of low overlap, it will likely proliferate. In LOW_{path} , the decline is steeper for Orders 2 and 3 shoots than Order 1 shoots (Figure 8). For Order 1 shoots in the $\text{LOW}_{\text{junctions}}$ partition, n_{over} has no evident effect on the expected number of daughter shoots. For Order 2 shoots in the $\text{LOW}_{\text{junctions}}$ partition, there is a sharp drop in the expected number of daughter shoots at n_{over} near 4 (as it declines from near 3 to near 0). For Order 3 shoots in the $\text{LOW}_{\text{junctions}}$ partition, the expected number of daughter shoots is near 0 for all shoots with at least one overlapping foliated shoot

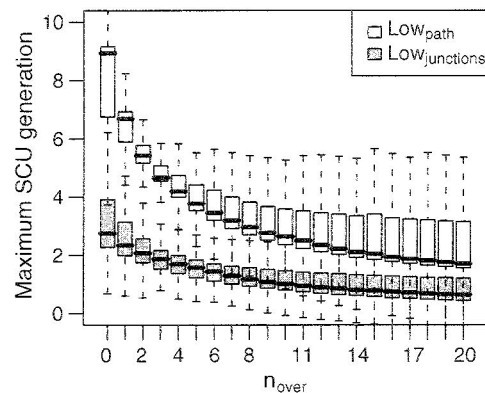


Figure 7. The maximum shoot cluster unit (SCU) generation (g^*) is both higher and decreases more steeply with increasing number of overlapping foliated shoots (n_{over}) for branches that tend to minimize mean path length to terminal active foliage (LOW_{path}) than branches that tend to minimize mean number of cumulative junctions to terminal foliage ($\text{LOW}_{\text{junctions}}$). For clarity, extreme values are excluded from the box plot, and the whiskers extend to 1.5 times the interquartile range.

(i.e., $n_{\text{over}} > 0$). These results for individual branch characteristics integrate to form an overall picture for morphogenesis for branches in each partition (Figure 9).

Summary of morphogenesis

Example branches from each partition appear similar early in branch development. However, beyond 25 branch years in LOW_{path} , the process of reiteration begins to dominate the branch pattern with the accumulation of higher foliage generations. These appear proximally along the major branching axis and in areas less occupied by other foliage. New epicormic shoots in areas already occupied by foliage are less likely to proliferate daughter shoots at a level sufficient to develop into a new SCU. Consequently, the emergence of epicormic shoots that develop into SCUs occurs in areas within the crown that are not occupied by other foliage. There is a threshold on reiteration relative to the foliage overlap, so that higher-generation SCUs do not occur at high overlap. In contrast, $\text{LOW}_{\text{junctions}}$ branches are not likely to regenerate foliage at high generations regardless of n_{over} . In the LOW_{path} partition, lower-generation foliage also continues to appear throughout the 90 years of branch growth, resulting from the release of buds that had been suppressed for decades. In contrast, for the $\text{LOW}_{\text{junctions}}$ partition the persistence of Order 2 axes represents a greater contribution to foliage amounts than does DAR. Longer lateral axes extend the path length to terminal foliage relative to the LOW_{path} branch, but there are fewer junctions between the main branch axis and terminal foliage (Figure 5).

Discussion

The modeling results that we present are significant in two ways. First, we approach the study of old trees with the focus

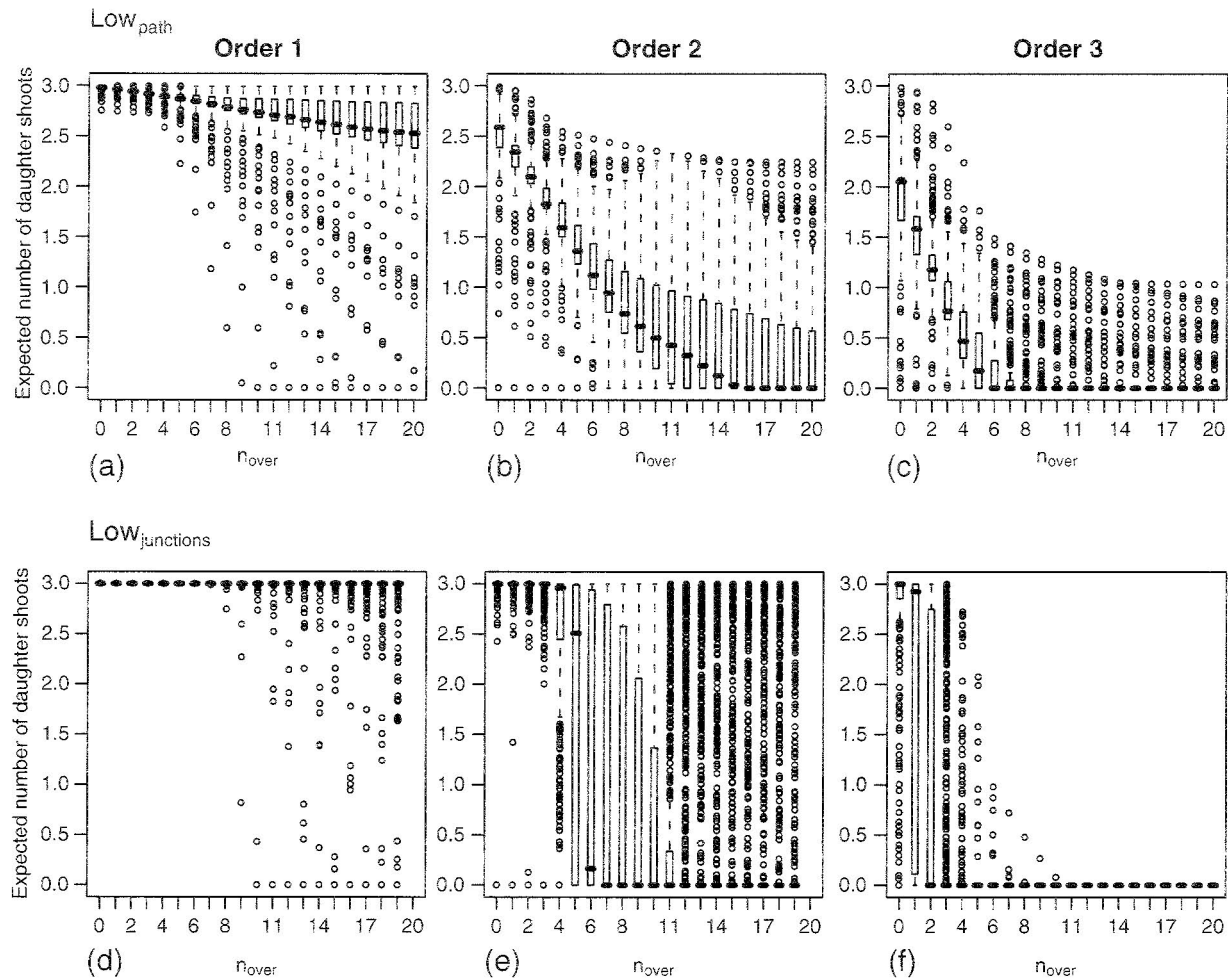


Figure 8. The expected number of daughter shoots decreases with increasing number of overlapping foliated shoots (n_{over}) for (a–c) branches that tend to minimize mean path length to terminal active foliage (LOW_{path}) and (d–f) branches that tend to minimize mean number of cumulative junctions to active foliage (LOW_{junctions}) for Orders 1, 2 and 3 shoots, respectively. LOW_{path} branches show a gradual decline in the expected number with increasing n_{over} whereas LOW_{junctions} branches show no relationship for Order 1 and threshold effects for Orders 2 and 3 at relatively low values of n_{over} . The box plot whiskers extend to 1.5 times the interquartile range, and points are outlying values beyond 1.5 times the interquartile range.

on how they are able to persist in the context of what limits their survival. Second, we illustrate a method that preserves the high dimensionality and complexity of a system in an explanation for how that system functions. In our multi-criteria optimization, we developed a Pareto optimal frontier of solutions with respect to eight criteria. The underlying model structure includes rules for foliage proliferation and bud release (Eqs. 1 and 2), and it constrains the feasible space in the optimization. The empirical criteria further constrain a portion of the solution set to those with shoot numbers consistent with observed pattern. We discovered two distinct morphologies as we evaluated patterns of branch morphogenesis along this Pareto optimal frontier (Figure 4). The solutions that tended to minimize U_{path} (LOW_{path}) also had patterns of branch morphogenesis that more closely replicated the observed *Pseudotsuga* branch pattern (Table 3). Through simulation analysis of this Pareto optimal frontier,

we suggest a theoretical synthesis for how the process of *Pseudotsuga* branch morphogenesis compensates for size-related constraints. This has three major parts.

- (1) The primary constraint on *Pseudotsuga* branch growth is the path length from the base of the branch to the terminal foliage; the process of DAR in old-growth *Pseudotsuga* reduces the mean path length to terminal foliage relative to other similar morphologies.
- (2) Old-growth *Pseudotsuga* exhibits, through DAR, an opportunistic architecture because successful proliferation of new epicormic shoots, and hence placement of new SCUs, is regulated by within-branch foliage overlap.
- (3) The process of DAR in *Pseudotsuga* is limited by the number of successive generations that can form and by the number of SCUs that are produced on the branch, as modified by the within-branch foliage overlap.

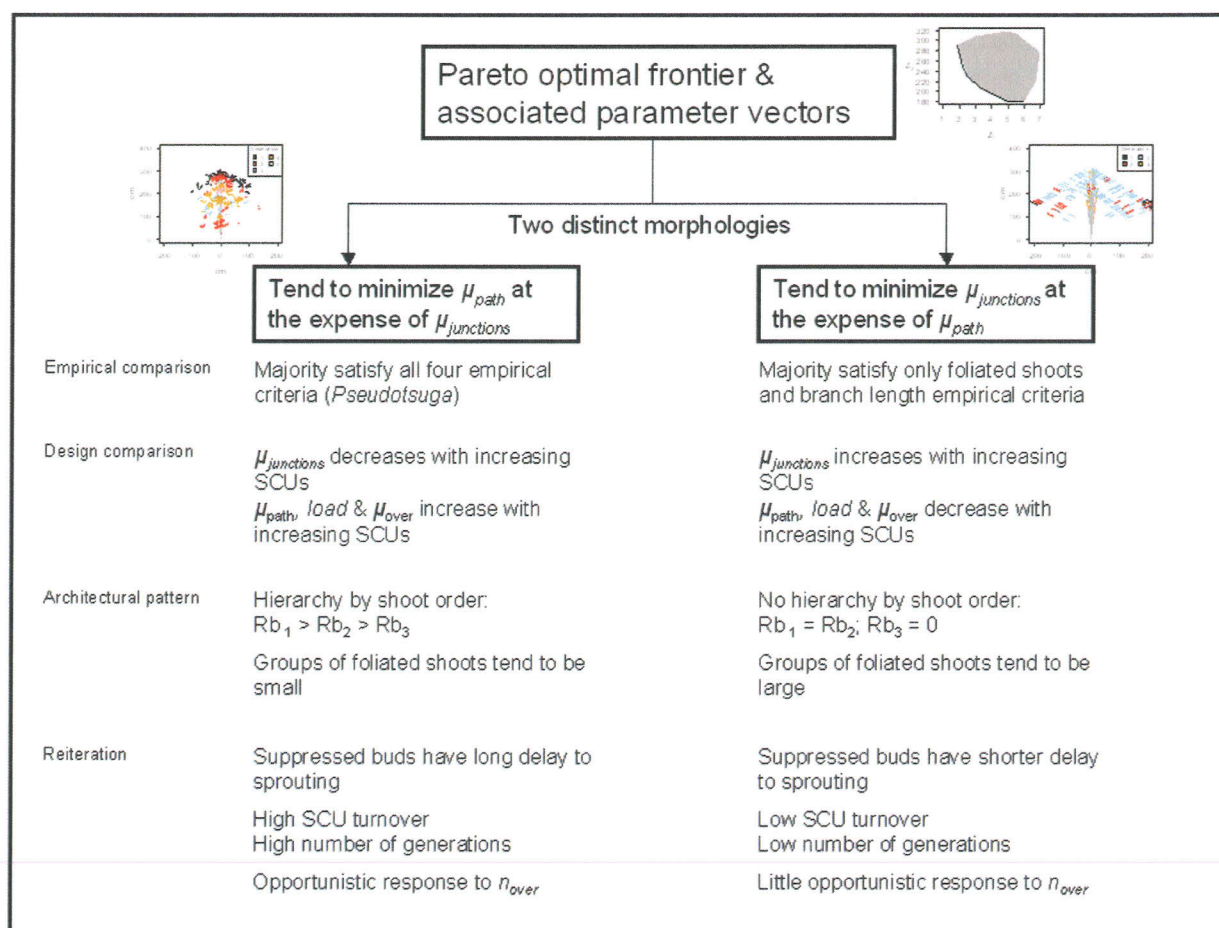


Figure 9. Summary of the contrast between the two distinct morphologies that are Pareto optimal with respect to eight criteria. The two criteria that clearly separate the morphologies are the mean path length to terminal active foliage (μ_{path}) and the mean number of cumulative junctions to terminal active foliage ($\mu_{junctions}$). The remaining design criteria are relative mechanical requirements (load) and mean number of overlapping foliated shoots (μ_{over}), and these influence the design details of each morphology. These morphologies are also differentiated by the number of shoot cluster units (SCUs) on the branch, as well as the basic architectural pattern. Rb is the mean number of daughter shoots, defined by the architectural order of the shoot (Orders 1, 2 or 3; Rb_1 , Rb_2 or Rb_3 , respectively). This figure appears in color in the online version of *Tree Physiology*.

We describe each of these components. Although this study was motivated by observations of old-growth *Pseudotsuga*, we also found that *Pseudotsuga* morphology is not the only solution to the persistence of old-growth trees. We describe features of the alternative morphology. In addition, although BRANCHPRO3 has been assessed against empirical measures, the Pareto optimal results we use to articulate each of the theoretical components should guide future empirical studies. To that end, we also suggest empirical contrasts that can be performed to evaluate the optimization results.

Primary constraint of path length

We find two distinct branch morphologies in the Pareto optimal space (Figure 4), which correspond to distinct clusters of parameterizations. The largest distinction in criteria performance between these two morphologies is between $\mu_{junctions}$ and μ_{path} (Figure 5). This provides evidence that hydraulic cri-

teria are the primary constraints that drive the observed division in branch morphology. Furthermore, from the empirical criteria, we know that the morphologies characteristic of the LOW_{path} parameter space more closely resemble the observed *Pseudotsuga* morphology than the morphologies characteristic of the $LOW_{junctions}$ partition (Table 3). The empirical criteria were not considered when partitioning the parameter space, and this result implies that the primary design criterion for old-growth *Pseudotsuga* branches is the mean path length from the base of the branch to the terminal foliage. This claim is consistent with systems analysis for a design with multiple criteria; it is usually a single criterion that dominates the major design specification and within that other criteria may influence design details (Niklas 1992, p. 20).

The relatively low values of μ_{path} in the LOW_{path} partition are accomplished through the simulated process of DAR. Branches in LOW_{path} tend to suppress buds for a longer time before they are released, relative to the time for suppression

of buds on branches in the $LOW_{junctions}$ partition (Table 3); this places potential new seus more proximally along major branch axes. Furthermore, the evident turnover of seus in LOW_{path} means that the lengths of SCUs main axes are restricted relative to SCUs on branches in the $LOW_{junctions}$ partition (Figure 4), which would reduce mean $f_{i,path}$. Lateral axes in LOW_{path} are also restricted in bifurcation relative to main axes (Table 3; Figure 8), and these show a greater degree of apical control than branches in the $LOW_{junctions}$ partition. The effect of low apical control and higher Order 2 bifurcation in the $LOW_{junctions}$ partition is that Order 2 axes are much longer for $LOW_{junctions}$ branches than for LOW_{path} branches, increasing the path length to terminal foliage.

Opportunistic architecture

Our simulated observations support the fact that DAR is an opportunistic process (Halle et al. 1978, Oldeman 1978, Tomlinson 1983, Begin and Filion 1999). The model results clearly demonstrate that DAR is the main feature of branch morphogenesis in the LOW_{path} partition, whereas increased lateral growth is the main feature of branch morphogenesis in the $LOW_{junctions}$ partition. This is shown by the greater number of SCUs on the simulated branches in LOW_{path} in contrast to the more regular pattern of growth as exhibited by branches in the $LOW_{junctions}$ partition (Figure 4). Reiteration begins with the release of a suppressed bud to form an epicormic shoot; in BRANCHPRO3, the success of the new epicormic shoot in producing daughter shoots varies with the local environment in which it emerges (e.g., on the number of foliated shoots that overlap it). In this sense, new epicormic shoots represent sampling points for the within-crown environment. If a bud forms a new epicormic shoot of high generation and foliage overlap, then it is unlikely to successfully produce new shoots. SCUs of higher generation will only form when there are favorable light conditions to be exploited. The continual decrease in expected number of daughters with increasing n_{over} for higher order shoots in LOW_{path} (Figure 8) also ensures that investment in lateral growth is relative to favorable light conditions, although not restricted to them. This then allows for an 'exploration' of the within-crown environment; shoots 'prosper' in areas of low overlap and senesce in areas of high overlap. There is evidence that the *Pseudotsuga* crown is characterized by a patchy light environment (Parker et al. 2002, Parker et al. 2004), and the opportunistic architecture may be an effective method to explore such a patchy environment.

Reiteration is limited

Two pieces of evidence in the optimization suggest that reiteration is limited. The first is the emergence of a maximum theoretical generation for SCUs (g^*) in branches characterized by the Pareto optimal set. The median value of the maximum generation at which a new seu can form among solutions in the LOW_{path} partition is 8.9, which is only slightly higher than the observed maximum of 7 for *Pseudotsuga*

(Table 3; Figure 7). This pattern emerged from the optimization of the four design criteria simultaneously, and the close correspondence between the values of g^* in the LOW_{path} partition and the maximum observed generation in *Pseudotsuga* implies that the limitation to reiteration in *Pseudotsuga* is related to the constraints represented by the design criteria in conjunction with the way in which the model regulates the proliferation of new epicormic shoots.

The value of g^* is driven by a restriction of bifurcation at junctions formed by the release of a bud from suppression; this implies that there is a significant hydraulic constriction at epicormic junctions relative to the junctions formed by regular sequential growth. Schulte and Brooks (2003) show that there is no evidence for hydraulic constriction at regular branch junctions for young *Pseudotsuga*, and in general hydraulic constrictions are measured at junctions of unequal diameter (Tyree and Ewers 1991). Eisner et al. (2002) observe that the ratio of conductivity between the branch and the trunk decreases with decreasing diameter ratio (branch diameter/trunk diameter). In *Pseudotsuga*, the difference in diameter at a junction could be greater for epicormic than for sequential junctions (e.g., compare diameter of new epicormic shoots to diameters of nearby lateral axes in Figure 1B) because of the timing of the junction formation, wherein the longer a bud is suppressed the greater is the disparity in diameter between the parent axis and the new epicormic axis. Furthermore, although the accumulation of generations is limited, the mean number of total junctions is higher in LOW_{path} relative to $LOW_{junctions}$. This implies that the constriction at regular junctions may be less severe for LOW_{path} relative to $LOW_{junctions}$.

The second evidence for a limitation to reiteration in *Pseudotsuga* is that the maximum number of SCUs observed in *Pseudotsuga* is comparable to the numbers of SCUs in the majority of solutions in the LOW_{path} partition. In *Pseudotsuga*, the maximum number of seus observed was 50, yet when branches were simulated without the constraints of the design criteria, Kennedy et al. (2004) found that hundreds of SCUs could accumulate. It would seem that the observed range of seus may result as a compromise between the number of cumulative junctions (which decreases with SCUs in the LOW_{path} partition) and the remaining three criteria (all of which increase with SCUs in the LOW_{path} partition).

Pseudotsuga is not the only solution

The multiple Pareto optimal solutions show two distinct branch morphologies, and the characteristics of the contrasting morphology ($LOW_{junctions}$) provide further insight into how an alternative process of morphogenesis enables persistence in the old-growth canopy (Figure 9). Kennedy (2002) and Kennedy et al. (2004) also simulated branch development in *Abies grandis* (Dougl. ex D. Don) Lindl. at the WRCCRF, and the overall branching pattern and values of bifurcation resemble those observed in the $LOW_{junctions}$ partition, though without epicormic proliferation. We propose

that the branch pattern characteristic of $Low_{junctions}$ resembles a more determinate branch pattern such as observed in the true firs like *A. grandis* (Figures 1A and 4B). Even though *Abies* is smaller and does not live as long as *Pseudotsuga* (maximum age of 500 years for *Abies* in contrast to 1200 years for *Pseudotsuga*), the two species do coexist for some time in the old-growth canopy. The ability of *Abies* to grow rapidly in relatively low light conditions enables it to either match or even exceed *Pseudotsuga* when simultaneously established or to quickly fill gaps; this means that it often co-occurs as a canopy dominant (Leverenz and Hinckley 1990), and it can achieve comparable heights (Van Pelt 2001). This procedure illustrates how different species exhibit diverse pathways to achieve sustained growth under a similar set of multiple, conflicting constraints. These pathways are influenced by the underlying physiology and life history of the species.

Suggestions for empirical evaluation of optimization results

BRANCHPRO3 was assessed against a set of empirical observations of *Pseudotsuga* morphology and based on the current state of knowledge of size-related constraints in trees. The search for empirical evidence, however, should not end with the modeling exercise, and the simulation results are most useful if they can guide future avenues of empirical observation (Schmitz 2000). For example, there are implications for theory component 1 with respect to the effect of extreme path length on water relations. Although the bulk of resistance to water flow is in the last meter of the hydraulic pathway (Tyree and Ewers 1991), the total resistance depends on the entirety of the pathway from roots to leaves; e.g., the resistance in the last meter for foliage at the end of a 50-m pathway may be more relatively severe than the resistance in the last meter for foliage at the end of a 10-m pathway. Ishii et al. (2008) show that, in large *Sequoia sempervirens* trees, foliage water potential during the wet season is lower (i.e., more negative) in the outer crown relative to the inner crown; their Figure 1A implies that the more negative water potential is more pronounced at the upper range of observed heights than the lower range. The effect of path length may be incrementally more severe at the top of large trees relative to smaller trees, the cause of which may include greater evaporative demand. We propose three empirical contrasts that can be made with old-growth *Pseudotsuga* to evaluate the effect of path length in the branches of large trees. (i) Douglas-fir in Southern California (*Pseudotsuga macrocarpa* (Vasey) Mayr) is able to achieve massive crown spread and branch lengths (Gause 1966, Bolton and Vogt 1969) but does not achieve similar height to *Pseudotsuga* in the Pacific Northwest. The increased hydraulic resistance with branch path length may not be as severe in the shorter trees. (ii) The effect of path length can be evaluated for young small *Pseudotsuga* trees relative to old large trees. This would determine whether the effect of path length differs between trees of varying age and height. (iii) The path lengths should be measured

in *Pseudotsuga* branches and compared to path lengths of *Abies*. Kennedy et al. (2004) observe that *A. grandis* branches tend to be shorter in length and younger in age than *Pseudotsuga*. Shorter branches would have reduced path lengths relative to those simulated in the $Low_{junctions}$ partition and would compensate for the trade-off between U_{path} and $U_{junctions}$. If empirical investigation shows that path length is not relatively constraining (i.e., does not affect water potentials with path lengths < 40 cm), then theory component 1 must be re-evaluated in the context of BRANCHPRO3. It may be that path length is correlated with another component of the branch morphology that provides a major design specification but was not calculated as a design criterion in BRANCHPRO3.

To evaluate whether there is a severe hydraulic constriction at new epicormic junctions, relative conductivity should be measured at epicormic junctions and compared to junctions formed by regular lateral growth. If a constriction is detected, then the factors that change the severity of the constriction should also be considered (e.g., the age of the bud or the relative diameter of the new epicormic shoot to its parent). If it is found that epicormic constrictions are no more severe than constrictions at lateral junctions or that the constriction is independent of epicormic generation, then there is likely an alternative explanation for the limitation of reiteration in *Pseudotsuga*.

The effect of the light environment on the process of reiteration should also be evaluated. The relationship we propose is that morphogenesis is an opportunistic process that responds to a variable within-crown light environment. This should be evaluated through observation of changes in the frequency of bifurcation and SCD production relative to the light environment experienced by within-crown shoots as well as the presence of neighboring foliage within branches of *Pseudotsuga*.

Multi-criteria optimization and theory development

We show that the use of multiple criteria is a powerful tool to explain variability in optimal behavior (Schmitz et al. 1998) when the relative contributions of the criteria to overall plant performance are unknown. Farnsworth and Niklas (1995) state that 'We have already indicated our belief that most, if not all, of the Pareto optimal solutions will be accepted in natural selection given a range of environmental circumstances and strategy options.' Rothley et al. (1997) provide evidence for this assertion in an optimal foraging example that shows how the actual behavior of grasshoppers moves along a Pareto optimal frontier of vigilance and energy intake depending on the predation pressure, and Vrugt et al. (2007) apply it to the flight paths of migratory birds (with preliminary evidence that the trade-off between energy spent and flight time corresponds to actual flight path choices). Given the difficulty in quantifying a single currency that reliably predicts optimal fitness across environments and life histories, a multi-criteria optimization tool allows us to char-

acterize the morphologies that correspond to Pareto optimal criteria combinations. This methodology explicitly accommodates variability in optimal behavior within the constraints of the model and optimization criteria. Using an FSM and four design criteria, we were able to uncover why an alternative morphology such as that characterized by *Abies* may also be successful in a similar environment. This was possible when multiple system features were integrated into a comprehensive explanation of an observed phenomenon.

The contrast between the two morphologies cannot be explained solely by the Pareto optimal results but also through the consideration of those results in the context of the environment and life history of the two species. Whereas *Pseudotsuga* is a long-lived pioneer that persists through all successional stages in the Pacific Northwest *Abies* tends to be a shade-tolerant secondary species that establishes and persists in a light-limited understory environment. *Abies* maintains a level of foliage in the understory, with sufficient photosynthetic capacity that allows it to emerge and respond to gaps formed by overstory disturbance. This is similar to the changes in expected bifurcation at threshold values of n_{over} whereby at zero foliage overlap all three shoot orders have the maximum number of expected daughter shoots in the $\text{LOW}_{\text{junctions}}$ partition but zero proliferation at higher n_{over} . For shade-acclimated understory trees, there is a lag between the exposure to increased light and increased growth (Tucker et al. 1987). This is an extreme response to changes in light conditions, which contrasts to the effective 'search' of a given environment as implied by the gradual response of simulated *Pseudotsuga*-like branches to the value of n_{over} . The differences in life history traits between *Pseudotsuga* and *Abies* are reflected in their locations along the Pareto optimal frontier, thereby demonstrating the advantage of using multi-criteria optimization.

For the paradigm of optimality theory in the study of complex biological phenomena, it is valuable to include the simultaneous optimization of multiple values that reflect the many interacting processes in organisms and ecosystems. This is particularly important under incomplete understanding of how multiple features integrate to determine whole-system functioning. This new component of the paradigm specifies that multiple features act as constraints and that the observed systems are consequences of their simultaneous and often synergistic effects. The individual system represents one among many possible solutions to the requirements imposed by the organism and the constraints.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

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