DESPOT, a process-based tree growth model that allocates carbon to maximize carbon gain

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Summary We present a new model of tree growth, DESPOT (Deducing Emergent Structure and Physiology Of Trees), in which carbon (C) allocation is adjusted in each time step to maximize whole-tree net C gain in the next time step. Carbon gain, respiration and the acquisition and transport of substitutable photosynthetic resources (nitrogen, water and light) are modeled on a process basis. The current form of DESPOT simulates a uniform, monospecific, self-thinning stand. This paper describes DESPOT and its general behavior in comparison to published data, and presents an evaluation of the sensitivity of its qualitative predictions by Monte Carlo parameter sensitivity analysis. DESPOT predicts determinate height growth and steady stand-level net primary productivity (NPP), but slow declines in aboveground NPP and leaf area index. Monte Carlo analysis, wherein the model was run repeatedly with randomly different parameter sets, revealed that many parameter sets do not lead to sustainable NPP. Of those that do lead to sustainable growth, the ratios at maturity of net to gross primary productivity and of leaf area to sapwood area are highly conserved.

Keywords: C allocation, forest productivity, optimality, photosynthesis, tree height, water relations.

Introduction

Many topical questions in tree ecophysiology involve structural and functional adaptation during growth. Tree growth may usefully be seen as a feedback loop between carbon (C) gain and C allocation: nitrogen (N) and water are captured by roots and transported by stems, light is captured by leaves and all three resources limit photosynthetic carbon gain—N and light constrain the sink strength of the photosynthetic apparatus for CO\(_2\) and water controls the supply of CO\(_2\) through stomatal conductance. Some of the carbon fixed and reduced in leaves is used to augment or replace roots, stems and leaves, shoring up photosynthetic resource capture and delivery and perpetuating the feedback cycle. Tree growth models link the component processes of this feedback loop and are thus powerful tools for understanding its adaptive regulation. When quantitatively accurate growth predictions are desired, empirical modeling is often most appropriate. However, when the aim is to predict growth under novel combinations of environmental conditions (e.g., future climates), or when the object of study is not growth outcomes but the underlying processes and constraints, it is preferable to use more generic and conservative principles.

Process laws are ideal for this purpose because they can be explained in terms of universal physico-chemical principles. Some aspects of tree growth can confidently be modeled on a process basis, including photosynthesis and the capture and delivery of photosynthetic resources. However, the processes that control carbon allocation are not well understood (Le Roux et al. 2001), so another generic principle is needed to simulate allocation. One strong candidate to fulfill this role is adaptation—the tendency for organisms to modify their structure and function in ways that improve performance (and ultimately reproductive success)—which is an embodiment of biology’s grand unified theory, natural selection. Teleonomic or goal-directed models attempt to capture adaptation by hypothesizing that, whatever the underlying mechanisms, regulatory processes optimize some quantifiable aspect of organism function. Teleonomic allocation models may even be preferable to process-based models if the aim is to understand the adaptive character of allocation itself and the structural and functional features that emerge from the adaptive regulation of allocation.

costs and benefits that are manifestly relevant to the feature of interest. For example, the ratio of leaf area to sapwood area is often evaluated in terms of hydraulic constraints, with the relevant functional balance being the maintenance of stomatal conductance and leaf water status (Shinozaki et al. 1964a, Whitehead et al. 1984, Valentine 1985, Mäkelä 1986, Magnani et al. 2000). This approach offers clarity and simplicity. It also has the advantage of creating analytical constraints—generic mathematical relationships that summarize, in a highly accessible form, what is known about conserved features of structural adaptation. Mathematical simplicity is a prerequisite for the incorporation of such powerful knowledge into predictive models, so its importance cannot be overstated.

However, the functional balance approach has some limitations and drawbacks. An analysis that focuses only on the processes that seem relevant may exclude other processes that significantly impact the costs and benefits of the feature in question if those impacts are sufficiently subtle or indirect to elude intuition. For example, C gain can be largely decoupled from the dynamics of any single resource because photosynthesis is limited by several substitutable resources (Mooney et al. 1978, Field et al. 1983, Reich et al. 1989, Cordell et al. 1999, Miller et al. 2001). This means that all functional C pools are economically interwoven: a change in allocation to one pool affects every other, and not only by mass balance, but also by changing the costs and benefits associated with allocation to those other pools. Replacing C gain by the more restrictive proxy goal of some particular functional balance precludes the full gamut of resource substitution, thus eliminating an important class of adaptive tactics that real trees may possess. As a result, patterns predicted on the basis of functional balance may not adequately reflect the constraints and opportunities experienced by a growing tree.

For these reasons, we believe there is merit in creating a model that accounts for the complex economic interdependencies among different C pools and photosynthetic resources by unifying all C allocation decisions under a single goal, and by using numerical optimization to identify growth trajectories that achieve that goal. This reduces the need to assume that certain tradeoffs are irrelevant to the feature of interest. Because it allows most structural features to emerge on their own, it also reduces the need for ad hoc allometric constraints on tree structure. Unlike functional balance, however, this approach is computationally highly intensive, so it is unlikely to yield mathematically simple predictions and it is unsuitable for use in large-scale predictive modeling. Its role, instead, is to clarify and improve the theoretical basis of simpler goal-directed approaches, which may then more confidently inform predictive modeling.

This paper presents a model of individual tree growth, DESPOT (Deducing Emergent Structure and Physiology Of Trees), that treats structural adaptation during growth as an optimization process in which the central currency is reduced C, the control parameters are C allocation fractions, the goal is to maximize growth (or, equivalently, net structural C gain or single-tree net primary production) and the underlying cost-benefit structure is implicit in a suite of process models for photosynthesis and for the acquisition and transport of substitutable photosynthetic resources (N, light and transpirable water). Constraints on structural geometry due to windthrow risk are treated with a mechanical and probabilistic approach. In this paper, we describe the general behavior of DESPOT, compare it with published data and evaluate the extent to which the model’s predictions are qualitatively robust by Monte Carlo parameter sensitivity analysis. The model itself is described in the Appendix. An accompanying paper (Buckley and Roberts 2006) discusses the model’s predictions for hydraulic compensation during height ($H$) growth.

**Overview of model assumptions**

For ease of reference, the model’s structure and core assumptions are summarized below. The reader is directed to the Appendix for more details.

**Carbon allocation**

In each time step, the total C increment available for structural growth is allocated to leaves, fine roots and radial, above-ground axial (height) and belowground axial (depth) sapwood production. A numerical algorithm finds the allocation fractions that maximize the C increment in the next time step.

**Carbon gain**

Photosynthesis is calculated with a big-leaf version of the Farquhar et al. (1980) photosynthesis model, based on electron transport and carboxylation capacities, photosynthetic irradiance and stomatal conductance.

**Nitrogen**

Photosynthetic capacity parameters are proportional to leaf N content, and canopy N content is simulated dynamically based on the balance between uptake by fine roots, losses due to senescence and N requirements for new increments of non-photosynthetic tissues with fixed C:N ratios. Soil N input is a fixed parameter.

**Light**

Leaf-level irradiance is a canopy average based on total light capture, which is calculated by Beer’s Law. The marginal response of canopy light capture to $H$ growth is calculated explicitly, assuming each canopy is rectangular in cross section and the stand is closed.

**Water**

Stomatal conductance is proportional to transpiration rate by a constant evaporative gradient. Canopy transpiration rate is assumed to be in steady-state with water movement from the soil to the site of evaporation, which in turn is calculated from Darcy’s Law. Independent resistance terms are used to describe the effects of fine roots, axial flow path length and sapwood area. The hydraulic gradient driving this flow is constrained by assuming fixed soil and leaf water potentials.
However, in the accompanying paper (Buckley and Roberts 2006), simulations are also performed in which leaf water potential declines enough to offset the $H$-related gravitational head.

**Carbon balance**

Senescence is modeled by tracking each individual increment of leaf, fine root and sapwood C and decrementing these increments over time based on the assumption of a Weibull distribution of tissue lifespans. Maintenance respiration is calculated independently for each C pool in fixed proportion to its N content; construction respiration is a fixed fraction of gross C gain minus respiration.

**Miscellaneous**

Most parameters were estimated to represent lodgepole pine (*Pinus contorta* Dougl. ex. Loud.). Windthrow risk, which is used to depress the apparent profitability of mechanically risky candidate allocation vectors, is estimated from canopy sail area, basal trunk diameter and coarse root anchorage depth, using a highly simplified mechanical model. Branching and tapering are not explicitly described. Instead, radial and axial sapwood increments are computed from their respective allocation fractions and the total wood C increment based on an empirical relationship between total stemwood volume (including branches) and radial and axial stem dimensions. This relationship, which implicitly captures aboveground branching and tapering patterns, is assumed to hold for coarse roots. The available ground area per tree and aspects of canopy geometry needed to estimate the benefit of $H$ growth are simulated by assuming the stand is uniform, and that it self-thins according to the $-3/2$ power law. All processes are simulated on an annual basis, so diurnal and seasonal effects such as temperature variation are ignored.

**Results and discussion**

**General behavior of the model**

Variables in the model are presented in Table 1. The simulations described here and illustrated in Figures 1 and 2 used parameter values estimated for lodgepole pine and, where possible, specifically for the lodgepole chronosequence studied by Ryan and Waring (1992) (Table 2). Therefore, comparable data from that chronosequence are shown with symbols in Figures 1 and 2, and Table 3 summarizes the comparison in tabulated format.

Despite the minimal degree to which C partitioning and $H$ growth are empirically constrained in the model, DESPOT predicts growth trajectories that compare fairly well with the observations of Ryan and Waring (1992) for 40- and 65-year-old lodgepole pine stands. In both the model and the data, leaf area index (LAI) increases quickly to around 10–12, and net and gross primary productivity (NPP and GPP, respectively) also peak by 40 years (at about 0.5 and 0.9 kg C m$^{-2}$ year$^{-1}$, respectively), whereas $H$ increases more steadily to around 10 m at 40 years, and around 12 m at 65 years (Figure 1, Table 3). However, $H$ growth in DESPOT tapers off at around 75 years and both NPP and GPP remain nearly constant. In contrast, Ryan and Waring (1992) found a further 45% increase in $H$ from 65 to 245 years, together with declines of 47 and 37%, respectively, in NPP and GPP (Figures 1a and 1c, Table 3). Many other data confirm that aboveground NPP (ANPP) generally declines with age in forest stands (see review by Ryan et al. 1997). DESPOT predicts a moderate de-

![Figure 1. Time courses of major tree and stand growth variables predicted by DESPOT for the parameter values given in Table 1 (thick lines), compared with analogous data (symbols connected by thin lines) observed by Ryan and Waring (1992) for a lodgepole pine chronosequence in Colorado, USA. (a) Height (solid lines and closed symbols) and basal area (broken lines and open symbols); (b) leaf area index (LAI); (c) gross primary productivity (GPP, broken lines and open symbols) and net primary productivity (NPP, solid lines and closed symbols); (d) above- and belowground NPP (ANPP, BNPP; solid and broken lines, respectively).](http://heronpublishing.com)
Table 1. Variables in DESPOT. “\( \text{minh}\{a,b,c\}\)” means the lesser root \( Q^2 - (a + b)Q + ab = 0 \). Subscripts for allocation fractions and carbon (C) pools are: \( l = \) leaves; \( r = \) fine roots; sw = sapwood; hw = heartwood; \( w = \) total wood; \( t = \) total C (sum of all pools); \( d = \) radial sw allocation; \( h = \) aboveground axial sw allocation; \( z = \) belowground axial sw allocation; and \( N = \) nitrogen.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Symbol</th>
<th>Units</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allocation fractions (( x = l,d,h,z ))</td>
<td>( a_x )</td>
<td>unitless</td>
<td>1</td>
</tr>
<tr>
<td>Leaf net CO(_2) assimilation rate</td>
<td>( A )</td>
<td>( \mu\text{mol C m}^{-2}\text{s}^{-1} )</td>
<td>6</td>
</tr>
<tr>
<td>A when RuBP carboxylation is limiting</td>
<td>( A_c )</td>
<td>( \mu\text{mol C m}^{-2}\text{s}^{-1} )</td>
<td>5</td>
</tr>
<tr>
<td>A when RuBP regeneration is limiting</td>
<td>( A_r )</td>
<td>( \mu\text{mol C m}^{-2}\text{s}^{-1} )</td>
<td>5</td>
</tr>
<tr>
<td>Supply equation for ( A )</td>
<td>( A_s )</td>
<td>( \mu\text{mol C m}^{-2}\text{s}^{-1} )</td>
<td>5</td>
</tr>
<tr>
<td>Single tree net primary production</td>
<td>( A_0 )</td>
<td>( \text{mol C year}^{-1} )</td>
<td>2</td>
</tr>
<tr>
<td>Single tree gross primary production</td>
<td>( A_t )</td>
<td>( \text{mol C year}^{-1} )</td>
<td>3</td>
</tr>
<tr>
<td>Canopy “absorbance”</td>
<td>( \alpha_c )</td>
<td>unitless</td>
<td>10–12</td>
</tr>
<tr>
<td>Intercellular CO(_2) mole fraction</td>
<td>( c_i )</td>
<td>( \mu\text{mol CO}_2\text{ mol}^{-1} )</td>
<td>5, 6</td>
</tr>
<tr>
<td>Carbon pools (( x = l,r,sw, hw, w, t ))</td>
<td>( C_x )</td>
<td>( \mu\text{mol CO}_2\text{ mol}^{-1} )</td>
<td>–</td>
</tr>
<tr>
<td>Basal trunk diameter</td>
<td>( D_b )</td>
<td>m</td>
<td>–</td>
</tr>
<tr>
<td>Leaf-level transpiration rate</td>
<td>( E )</td>
<td>mmol H(_2)O m(^{-2})s(^{-1} ) ( E_i/L \cdot 10^3 )</td>
<td></td>
</tr>
<tr>
<td>Whole-tree transpiration rate</td>
<td>( E_t )</td>
<td>mmol H(_2)O s(^{-1} )</td>
<td>7</td>
</tr>
<tr>
<td>Total leaf conductance to CO(_2)</td>
<td>( g_{lc} )</td>
<td>( \text{mol m}^{-2}\text{s}^{-1} )</td>
<td>( g_i/(1.6 + 1.37r_w g_s) )</td>
</tr>
<tr>
<td>Stomatal conductance to H(_2)O</td>
<td>( g_s )</td>
<td>mmol ( \text{m}^{-2}\text{s}^{-1} )</td>
<td>( E_i/(D - r_w E) )</td>
</tr>
<tr>
<td>Canopy projected ground area of one tree</td>
<td>( G )</td>
<td>( \text{m}^2 )</td>
<td>( 1/\rho_n )</td>
</tr>
<tr>
<td>Stand-level gross primary productivity</td>
<td>( GPP )</td>
<td>( \text{kg C m}^{-2}\text{year}^{-1} )</td>
<td>0.012 ( \rho_s A_i )</td>
</tr>
<tr>
<td>Vertical span of axial flow path length</td>
<td>( h )</td>
<td>m</td>
<td>( H(1 - 0.5 \text{ LCR}) + \pi/2^2 )</td>
</tr>
<tr>
<td>Tree height</td>
<td>( H )</td>
<td>m</td>
<td>–</td>
</tr>
<tr>
<td>Leaf-level incident irradiance</td>
<td>( I )</td>
<td>( \mu\text{mol m}^{-2}\text{s}^{-1} ) ( I_i/L )</td>
<td></td>
</tr>
<tr>
<td>Whole-tree light capture</td>
<td>( I_i )</td>
<td>( \mu\text{mol s}^{-1} )</td>
<td>10–12</td>
</tr>
<tr>
<td>Potential electron transport rate</td>
<td>( J )</td>
<td>( \mu\text{mol e}^{-}\text{m}^{-2}\text{s}^{-1} )</td>
<td>( \text{minh}{J_m \phi I B_i} )</td>
</tr>
<tr>
<td>Electron transport capacity</td>
<td>( J_m )</td>
<td>( \mu\text{mol e}^{-}\text{m}^{-2}\text{s}^{-1} )</td>
<td>( \phi/N )</td>
</tr>
<tr>
<td>Leaf-specific hydraulic conductance</td>
<td>( K_L )</td>
<td>mmol H(_2)O m(^{-2})s(^{-1})MPa(^{-1} )</td>
<td>( E_i\text{MP} )</td>
</tr>
<tr>
<td>Axial flow path length</td>
<td>( l )</td>
<td>( \text{m} )</td>
<td>Text after 7</td>
</tr>
<tr>
<td>Leaf area, projected leaf area</td>
<td>( L, L_p )</td>
<td>( \text{m}^2 )</td>
<td>SLA ( C_i ), ( \text{L}/3.34 )</td>
</tr>
<tr>
<td>Stand-level leaf area index</td>
<td>( LAI )</td>
<td>( \text{m}^2\text{m}^{-2} )</td>
<td>( \rho \text{r}_p )</td>
</tr>
<tr>
<td>Leaf photosynthetic N content</td>
<td>( N )</td>
<td>( \text{mmol N m}^{-2} )</td>
<td>( N/L )</td>
</tr>
<tr>
<td>Stand-level net primary productivity</td>
<td>( NPP )</td>
<td>( \text{kg C m}^{-2}\text{year}^{-1} )</td>
<td>0.012 ( \rho_s A_i )</td>
</tr>
<tr>
<td>Canopy photosynthetic N content</td>
<td>( N_t )</td>
<td>( \text{mmol N} )</td>
<td>8, 9</td>
</tr>
<tr>
<td>Pressure gradient from soil to leaf</td>
<td>( \Delta P )</td>
<td>MPa</td>
<td>7</td>
</tr>
<tr>
<td>Probability of stem breakage</td>
<td>( p_b )</td>
<td>unitless</td>
<td>24</td>
</tr>
<tr>
<td>Probability of uprooting</td>
<td>( p_u )</td>
<td>unitless</td>
<td>24</td>
</tr>
<tr>
<td>Canopy laminar resistance</td>
<td>( r_i )</td>
<td>( \text{mol H}_2\text{O}^{-1}\text{s MPa}^{-1} )</td>
<td>( r_u/L )</td>
</tr>
<tr>
<td>Soil–xylem hydraulic resistance</td>
<td>( r_s )</td>
<td>( \text{mol H}_2\text{O}^{-1}\text{s MPa}^{-1} )</td>
<td>7</td>
</tr>
<tr>
<td>Axial (xylem) hydraulic resistance</td>
<td>( r_x )</td>
<td>( \text{mol H}_2\text{O}^{-1}\text{s MPa}^{-1} )</td>
<td>7</td>
</tr>
<tr>
<td>Leaf respiration in the day</td>
<td>( R_l )</td>
<td>( \mu\text{mol CO}_2\text{ m}^{-2}\text{s}^{-1} )</td>
<td>0.01 ( V_m )</td>
</tr>
<tr>
<td>Maintenance respiration</td>
<td>( R_m )</td>
<td>( \text{mol C year}^{-1} )</td>
<td>2</td>
</tr>
<tr>
<td>Stand density</td>
<td>( \rho_s )</td>
<td>trees \text{m}^{-2}</td>
<td>21</td>
</tr>
<tr>
<td>Sapwood area</td>
<td>( S )</td>
<td>( \text{m}^2 )</td>
<td>20</td>
</tr>
<tr>
<td>Maximum RuBP carboxylation velocity</td>
<td>( V_m )</td>
<td>( \mu\text{mol CO}_2\text{ m}^{-2}\text{s}^{-1} )</td>
<td>( J_m/2.1 )</td>
</tr>
<tr>
<td>Crown width</td>
<td>( W )</td>
<td>m</td>
<td>( G^{1/2} (\approx 1/\rho_s^{1/2}) )</td>
</tr>
<tr>
<td>Rooting depth</td>
<td>( Z )</td>
<td>m</td>
<td>–</td>
</tr>
</tbody>
</table>

clines in ANPP of around 15% from 50 to 250 years, but this is countered by an increase in belowground NPP (BNPP) (Figure 1d) driven by changes in windthrow risk.

Windthrow risk

One emergent feature of the growth trajectories predicted by DESPOT is a balance between the probabilities of windthrow due to stem breakage and uprooting (\( p_b \) and \( p_u \) respectively). The model chooses allocation fractions that maximize the product of net C gain with the complement of the greater of \( p_b \) and \( p_u \) (see Appendix for details), so these probabilities can be thought of as a risk tax to discourage the production of mechanically untenable growth forms, such as excessively top-heavy or tall and thin trunks. Figure 2 shows that \( p_b \) and \( p_u \) increase rapidly and in concert during early \( H \) growth, causing the risk tax to exceed 14%. Height growth then slows as its perceived benefit for light competition declines as a result of stand thinning and as its hydraulic costs increase. The risk tax then declines until \( H \) growth ceases. The risk of stem breakage continues to decline because its dependence on the third power
of basal trunk diameter \((D_b; \text{Equation A22})\) allows the stem’s bending resistance to outpace the increase in turning moment caused by increasing canopy sail area, which results from stand thinning. However, the uprooting risk continues to increase because the costs of mitigating that risk by axial growth of woody roots, such as hydraulic path length, sapwood respiration and diversion of C from other pools, are too large to justify total mitigation of uprooting risk.

Broad-spectrum parameter sensitivity analysis

It was not our intention to produce a model for lodgepole pine, but instead to create a generic theoretical structure for studying tree growth. Therefore, to determine how qualitatively robust DESPOT’s general behavior is, we performed a broad-spectrum Monte Carlo parameter sensitivity analysis in which all parameters were varied randomly by ± 25% of the standard values given in Table 2 (except for live crown ratio, \((LCR)\), which was capped at 1.0), among 100 simulations, each 200 years in length.

The numerical values predicted at 200 years for most major tree and stand variables, such as tree \(H\), LAI, NPP and GPP, varied widely among simulations. For example, \(H\) at 200 years ranged from 0.5 to 45 m; NPP ranged from zero to 0.82 kg C m\(^{-2}\) year\(^{-1}\); and all-sides LAI ranged from zero to 15.7. However, several qualitative results were conserved among parameter sets. In 52 of 100 simulations, NPP had declined to zero by 200 years, but in other simulations productivity achieved a sustainable maximum. In all simulations, \(H\) growth eventually reached a maximum.

Table 2. Parameters in DESPOT. Source notations are as follows: (1) de Pury et al. (1997); (2) Ryan and Waring (1992); (3) Murty et al. (1996); (4) Whitehead et al. (1984); (5) observations by the authors; (6) Ryan (1991); (7) Dewar and McMurtrie (1996); (8) Ryan (1989); (9) Yoder et al. (1994); (10) Dougherty et al. (2003); (*) see details in Parameter estimation in Appendix; and (†) assumption.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Value</th>
<th>Units</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Effective solar angle (zenith = 0°)</td>
<td>(\beta)</td>
<td>54.5</td>
<td>degrees</td>
<td>+</td>
</tr>
<tr>
<td>Ambient CO(_2) mole fraction</td>
<td>(c_a)</td>
<td>370</td>
<td>(\mu\text{mol CO}_2\ \text{mol}^{-1})</td>
<td>†</td>
</tr>
<tr>
<td>Nitrogen cost of electron transport capacity</td>
<td>(\chi_j)</td>
<td>1.9</td>
<td>(\mu\text{mol e}^{-}\ \text{s}^{-1}(\text{mmol N})^{-1})</td>
<td>1</td>
</tr>
<tr>
<td>Leaf-to-air water vapor mole fraction gradient</td>
<td>(D)</td>
<td>0.015</td>
<td>(\text{mol H}_2\text{O mol}^{-1})</td>
<td>†</td>
</tr>
<tr>
<td>Weibull parameter for senescence failure rates</td>
<td>(\varepsilon)</td>
<td>4</td>
<td>unitless</td>
<td>†</td>
</tr>
<tr>
<td>Quantum yield of electrons from incident irradiance</td>
<td>(\phi)</td>
<td>0.3</td>
<td>(\text{e}^{-}\ \text{photon}^{-1})</td>
<td>†</td>
</tr>
<tr>
<td>Construction respiration fraction</td>
<td>(f_c)</td>
<td>0.22</td>
<td>unitless</td>
<td>2</td>
</tr>
<tr>
<td>Fraction of N recycled from leaves</td>
<td>(\gamma_t)</td>
<td>0.5</td>
<td>unitless</td>
<td>3</td>
</tr>
<tr>
<td>Fraction of N recycled from sapwood</td>
<td>(\gamma_{sw})</td>
<td>0.6</td>
<td>unitless</td>
<td>3</td>
</tr>
<tr>
<td>Solar beam irradiance</td>
<td>(I_s)</td>
<td>1915</td>
<td>(\mu\text{mol m}^{-2}\ \text{s}^{-1})</td>
<td>†</td>
</tr>
<tr>
<td>Fine root C per unit ground area at half max N uptake</td>
<td>(k_L)</td>
<td>16.0</td>
<td>(\text{mol C m}^{-2})</td>
<td>†</td>
</tr>
<tr>
<td>Light extinction coefficient</td>
<td>(k'L)</td>
<td>0.5</td>
<td>(\mu\text{mol CO}_2\ \text{mol}^{-1})</td>
<td>1</td>
</tr>
<tr>
<td>Soil–xylem hydraulic conductance per mol fine root C</td>
<td>(k_{ue})</td>
<td>8.3 \times 10^{-4}</td>
<td>(\text{mol H}_2\text{O MPa}^{-1}\text{mol C}^{-1})</td>
<td>†</td>
</tr>
<tr>
<td>Sapwood permeability</td>
<td>(k_s)</td>
<td>2.05 \times 10^{-12}</td>
<td>(\text{mol m}^{-2})</td>
<td>3</td>
</tr>
<tr>
<td>Effective Michaelis constant for Rubisco</td>
<td>(K')</td>
<td>746</td>
<td>(\mu\text{mol CO}_2\ \text{mol}^{-1})</td>
<td>1</td>
</tr>
<tr>
<td>Live crown ratio</td>
<td>(LCR)</td>
<td>0.84</td>
<td>unitless</td>
<td>5</td>
</tr>
<tr>
<td>Leaf and fine root maintenance respiration per unit N</td>
<td>(n_e)</td>
<td>0.041</td>
<td>(\text{mol C year}^{-1}(\text{mmol N})^{-1})</td>
<td>6</td>
</tr>
<tr>
<td>Nitrogen content of fine roots</td>
<td>(n_{fr})</td>
<td>17</td>
<td>(\text{mmol N (mol C)}^{-1})</td>
<td>7</td>
</tr>
<tr>
<td>Nitrogen content of sapwood</td>
<td>(n_{sw})</td>
<td>1.2</td>
<td>(\text{mmol N (mol C)}^{-1})</td>
<td>3</td>
</tr>
<tr>
<td>Colimitation parameter for photosynthesis</td>
<td>(\Theta_{A})</td>
<td>0.9</td>
<td>unitless</td>
<td>†</td>
</tr>
<tr>
<td>Colimitation parameters for potential e transport</td>
<td>(\Theta_{J})</td>
<td>0.9</td>
<td>unitless</td>
<td>†</td>
</tr>
<tr>
<td>Boundary layer resistance to water vapor</td>
<td>(r_{bw})</td>
<td>0.5</td>
<td>(\text{m}^2\ \text{s} \text{mol}^{-1})</td>
<td>†</td>
</tr>
<tr>
<td>Leaf laminar resistance parameter</td>
<td>(r_{la})</td>
<td>50</td>
<td>(\text{MPa s} (\text{mol H}_2\text{O})^{-1})</td>
<td>†</td>
</tr>
<tr>
<td>Wood carbon density</td>
<td>(\rho_{sw})</td>
<td>1.4 \times 10^4</td>
<td>(\text{mol C m}^{-3})</td>
<td>8</td>
</tr>
<tr>
<td>Self-thinning parameter</td>
<td>(\rho_{sc})</td>
<td>49</td>
<td>(\text{trees m}^{-2} (\text{mol C})^{2/3})</td>
<td>2</td>
</tr>
<tr>
<td>Initial stand density</td>
<td>(\rho_{si})</td>
<td>5</td>
<td>(\text{trees m}^{-2})</td>
<td>†</td>
</tr>
<tr>
<td>Leaf area per unit C</td>
<td>SLA</td>
<td>0.091</td>
<td>(\text{m}^2 (\text{mol C})^{-1})</td>
<td>3</td>
</tr>
<tr>
<td>Median leaf lifespan</td>
<td>(\tau_1)</td>
<td>8.3</td>
<td>year</td>
<td>3</td>
</tr>
<tr>
<td>Median fine root lifespan</td>
<td>(\tau_f)</td>
<td>1.0</td>
<td>year</td>
<td>3</td>
</tr>
<tr>
<td>Median sapwood lifespan</td>
<td>(\tau_{sw})</td>
<td>14</td>
<td>year</td>
<td>5</td>
</tr>
<tr>
<td>Total N input per unit ground area</td>
<td>(U_0)</td>
<td>660</td>
<td>(\text{mmol N year}^{-1}\ \text{m}^{-2})</td>
<td>†</td>
</tr>
<tr>
<td>Extreme value index for windspeeds</td>
<td>(\omega)</td>
<td>–0.25</td>
<td>unitless</td>
<td>10</td>
</tr>
<tr>
<td>Windthrow risk parameter for stem breakage</td>
<td>(w_b)</td>
<td>1.15 \times 10^5</td>
<td>unlitess</td>
<td>†</td>
</tr>
<tr>
<td>Windthrow risk parameter for uprooting</td>
<td>(w_u)</td>
<td>2.3</td>
<td>(\text{m}^{-1})</td>
<td>†</td>
</tr>
<tr>
<td>Parameter relating trunk dimensions to volume</td>
<td>(\xi)</td>
<td>0.299</td>
<td>(\text{m}^3\ \text{m}^{-3})</td>
<td>†</td>
</tr>
<tr>
<td>Time integration factor</td>
<td>(\gamma)</td>
<td>3.1</td>
<td>(\text{mol year}^{-1}(\text{mol s}^{-1})^{-1})</td>
<td>†</td>
</tr>
<tr>
<td>Leaf water potential</td>
<td>(\psi_f)</td>
<td>–1.5</td>
<td>(\text{MPa})</td>
<td>9</td>
</tr>
<tr>
<td>Soil water potential</td>
<td>(\psi_s)</td>
<td>–0.5</td>
<td>(\text{MPa})</td>
<td>9</td>
</tr>
</tbody>
</table>
ceased and both intercellular CO₂ mole fraction (ci) and stomatal conductance (gs) declined during H growth.

At 200 years, NPP and GPP were linearly correlated with a slope of 0.495 (Figure 3a), which is fairly close to the value (0.47) found by Waring et al. (1998) for a range of species. Dewar et al. (1999) showed that strong conservation in the ratio of NPP/GPP could be explained by substrate limitation for respiration. However, DESPOT predicts that a similar relationship should emerge even when respiratory coefficients (maintenance respiration per unit tissue N, (vm)), and construction respiration fraction, (fc)) vary randomly among simulated trees, which suggests that the adaptive regulation of C allocation may also be partly responsible for this conserved emergent property of tree physiology.

Sapwood area and projected leaf area (S(cm²) and L(m²), respectively) at 200 years were also linearly correlated among parameter sets, with the best fit provided by a power law with an exponent close to unity: L=0.238S0.9995 (Figure 3b). This is similar to the slope of 0.23 found by Whitehead et al. (1984) for lodgepole pine, but higher than some other values: cf. 0.19 (Dean and Long 1986), 0.13 (Kaufmann and Troendle 1981), 0.06–0.17 (Pearson et al. 1984) (values from the latter two references were divided by 3.34 to estimate projected area).

Summary of predictions

Several of the model’s qualitative predictions seem intuitive, but many others are either non-intuitive or manifestly inaccurate. In the hope of promoting discussion or experimentation to improve our understanding of the goals and constraints that shape tree growth and thus also to improve the logical structure of DESPOT, Table 4 summarizes some of the model’s salient predictions (several of these predictions are drawn from simulations described in the accompanying paper, Buckley and Roberts 2006). The predictions are labeled by the degree to which they seem intuitive (based on our own opinions and on discussions with colleagues) and by the degree to which they are accurate (if known or applicable). The most significant predictions that are either inaccurate or counterintuitive are: (1) that NPP reaches a sustainable maximum and does not subsequently decline; (2) that H growth ceases at around the same time that NPP stabilizes; (3) that the ratio of L/S declines with H during most of H growth; and (4) that arbitrary reductions in the accuracy or precision of the model’s optimization algorithm cause sustained H growth. (The latter two predictions are from Buckley and Roberts 2006.)

The accompanying paper (Buckley and Roberts 2006) discusses possible explanations for divergence of DESPOT’s qualitative predictions from observations. Two of these possibilities seem most likely to explain why the model fails to predict indefinite H growth and declining productivity: failure of the assumption that the processes controlling C allocation in real trees achieve the precise numerical optima identified by our computer simulations and failure of the assumption that the goal of C allocation is always and simply to maximize C gain.

Why is DESPOT novel?

Our model is novel in its synthesis of three major features: (1) the teleonomic goal (to maximize C gain); (2) a comprehensive cost-benefit structure for C gain based on process models for photosynthesis and for the delivery of three major substitutable photosynthetic resources, plus an economic treatment of windthrow risk; and (3) the lack of prescribed relationships between emergent structural or physiological

Table 3. Comparison between DESPOT predictions and observations (RW) by Ryan and Waring (1992) of a lodgepole chronosequence in Colorado. Abbreviations: LAI = leaf area index; NPP = net primary productivity; GPP = gross primary productivity; and C = carbon.

<table>
<thead>
<tr>
<th>Quantity</th>
<th>Age (year)</th>
<th>Height (m)</th>
<th>Basal area (m² ha⁻¹ year⁻¹)</th>
<th>LAI (kg C m⁻²)</th>
<th>NPP (kg C m⁻² year⁻¹)</th>
<th>GPP (kg C m⁻²)</th>
<th>Total biomass C (kg C m⁻²)</th>
<th>Stand density (stems ha⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DESPOT</td>
<td>40</td>
<td>9.9</td>
<td>52.5</td>
<td>9.9</td>
<td>0.51</td>
<td>0.92</td>
<td>4.8</td>
<td>7171</td>
</tr>
<tr>
<td></td>
<td>65</td>
<td>12.1</td>
<td>60.9</td>
<td>10.7</td>
<td>0.51</td>
<td>0.92</td>
<td>6.9</td>
<td>3583</td>
</tr>
<tr>
<td></td>
<td>245</td>
<td>12.3</td>
<td>174.3</td>
<td>10.4</td>
<td>0.51</td>
<td>0.93</td>
<td>20.5</td>
<td>405</td>
</tr>
<tr>
<td>RW</td>
<td>40</td>
<td>10.3</td>
<td>35.2</td>
<td>12.3</td>
<td>0.47</td>
<td>0.92</td>
<td>6.2</td>
<td>4367</td>
</tr>
<tr>
<td></td>
<td>65</td>
<td>11.9</td>
<td>40.4</td>
<td>12.1</td>
<td>0.42</td>
<td>0.84</td>
<td>7.6</td>
<td>3311</td>
</tr>
<tr>
<td></td>
<td>245</td>
<td>17.4</td>
<td>44.7</td>
<td>7.7</td>
<td>0.25</td>
<td>0.58</td>
<td>9.0</td>
<td>1067</td>
</tr>
</tbody>
</table>

Figure 2. Time courses of height (solid line) and windthrow risk (pu (dotted line) = probability of uprooting; and pb (dashed line) = probability of stem breakage) during height growth, predicted by DESPOT for the parameters values given in Table 1. Structural regulation by DESPOT balanced the probabilities of uprooting and breakage, so that they were nearly equal until an age of approximately 60 years. Note the axis break and change of scale at 100 years.
We are unaware of any model that includes all of these features.

Some growth models predict C allocation based on empirical allocation fractions (e.g., G’DAG, Comins and McMurtrie 1993) or a hierarchy of sink priorities (e.g., FOREST-BGC, Running and Coughlan 1988, TREGRO, Weinstein et al. 1991). Many other models are teleonomic—they assume allocation is regulated to achieve some goal—but the specified goal varies widely among models. For example, the WBE model (West et al. 1999) supposes that the goal of biomass partitioning is to minimize hydraulic resistance per unit of light-capturing leaf area and King (1990, 1993) evaluated H growth with respect to the goal of maximizing wood production.

Several teleonomic models assume, like DESPOT, that the goal of C allocation is to maximize C gain or growth (e.g., Reynolds and Thornley 1982, Johnson and Thornley 1987, Hari et al. 1990, Hof et al. 1990, Hilbert and Reynolds 1991, Chen and Reynolds 1997). However, none of these models also account for the effects of the three key substitutable resources on photosynthetic C gain. For example, Hilbert and Reynolds (1991) maximized C gain by varying leaf N content using a biochemical model of photosynthesis, but their analysis assumed constant $c_i$, thus excluding costs and benefits of C allocation for water capture and transport. The model of Hari et al. (1990) explicitly optimized C gain and included responses of photosynthesis to both N and water, but excluded light capture and constrained some aspects of C allocation with an assumption derived from the pipe-model theory. Conversely, of the models that do account for the three substitutable photosynthetic resources, none optimizes C allocation to maximize C gain. (For a comprehensive review of C allocation models, see Le Roux et al. 2001, which lists models according to the methods of simulating C gain and allocation.)

In many other teleonomic models, the goal that drives allocation involves some type of functional balance. Davidson (1969) suggested that plants adjust their root:shoot ratio to balance nutrient uptake rate and C gain and Thornley (1972a) showed that this structural balance maximizes growth in a simple model. Although other analyses (Reynolds and Thornley 1982, Mäkelä and Sievanen 1987) have since shown that biomass partitioning must vary over time to maximize growth, the functional balance paradigm persists. There are at least two reasons for this. First, it greatly simplifies modeling—each postulated balance removes at least one degree of freedom from the simulation, because it constrains at least two variables with respect to one another. For example, many models use a constrained relationship between $L$ and $S$ as a convenient way to constrain C allocation (Valentine 1985, Mäkelä 1986, Mäkelä 1999, Valentine 1999, Lo et al. 2001, Battaglia et al. 2004). This is often justified by the pipe-model theory of Shinozaki et al. (1964a, 1964b), which involves a functional balance between hydraulic supply and demand. Second, there is some mechanistic basis for the functional balance concept. Although the processes controlling C allocation are not well known, evidence suggests C is allocated in proportion to sink strength (Thornley 1972b, Dewar et al. 1998, Le Roux et al. 2001). This would yield a homeostatic balance between sink and source strength in the steady state. Similarly, Chen and Reynolds (1997) showed that a model based on dynamic coordination of C and water limitations on growth rate predicted similar, and in some cases identical, growth trajectories as did models based on optimization.

However, functional balance does not necessarily reflect optimal adaptation. Mäkelä (1986) and Valentine (1985) showed

![Figure 3. Two generic relationships that emerged from broad-spectrum Monte Carlo parameter sensitivity analysis, in which every parameter in Table 2 was varied randomly within a uniform distribution ranging between 75% and 125% of the value given in Table 2 (except live crown ratio (LCR), which was capped at 1.0), in 100 different simulations. Each value represents a different parameter set and hence a different simulated tree and environment, sampled at an age of 200 years. Cases where NPP (net primary productivity) was less than 0.01 kg C m$^{-2}$ year$^{-1}$ at 200 years are not shown. (a) GPP (gross primary productivity) vs. NPP (the broken line is a linear regression with equation NPP = 0.495 GPP + 0.031 and $r^2 = 0.955$) and (b) leaf area ($L$) vs. sapwood area ($S$) (the broken line is a power function fitted to the values shown, with equation $L = 0.238 S^{0.9995}$ and $r^2 = 0.984$).](http://heronpublishing.com)
Table 4. Some major qualitative predictions from DESPOT and the degree to which they seem intuitive (to the authors) and accurate. Predictions marked by an asterisk (*) are from simulations described and discussed in the accompanying paper (Buckley and Roberts 2006); of those predictions, the two involving “arbitrary constraints on C allocation” are from simulations in which the accuracy or precision of the allocation optimization algorithm was artificially reduced. For predictions concerning model exercises with no obvious real-world analogue, accuracy is given as “n/a”. Abbreviations: $H = \text{height}$; $c_i = \text{intercellular } \text{CO}_2 \text{ mole fraction}$; and $g_s = \text{stomatal conductance to water vapor}$. Abbreviations: NPP = net primary productivity; and GPP = gross primary productivity.

<table>
<thead>
<tr>
<th>Prediction</th>
<th>Intuitiveness</th>
<th>Accuracy</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Productivity</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ratio of NPP/GPP is somewhat conserved and close to 0.5</td>
<td>Weakly intuitive</td>
<td>Accurate</td>
</tr>
<tr>
<td>Ratio of NPP/GPP decreases weakly with increasing $H$</td>
<td>Weakly or non-intuitive</td>
<td>Uncertain</td>
</tr>
<tr>
<td>in broad-spectrum Monte Carlo simulation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>NPP reaches sustainable maximum</td>
<td>Nonintuitive</td>
<td>Inaccurate</td>
</tr>
<tr>
<td>Arbitrary constraints on C allocation reduce NPP$^*$</td>
<td>Intuitive</td>
<td>n/a</td>
</tr>
<tr>
<td><strong>Height growth</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$c_i$ and $g_s$ decline with $H$ during $H$ growth</td>
<td>Intuitive</td>
<td>Usually accurate</td>
</tr>
<tr>
<td>Leaf area: sapwood area ratio declines with $H$ during most of $H$ growth$^*$</td>
<td>Counterintuitive</td>
<td>Varies; more often inaccurate</td>
</tr>
<tr>
<td>Height growth is clearly determinate</td>
<td>Nonintuitive</td>
<td>Usually inaccurate</td>
</tr>
<tr>
<td>Arbitrary constraints on C allocation cause sustained $H$ growth$^*$</td>
<td>Nonintuitive</td>
<td>n/a</td>
</tr>
</tbody>
</table>

What is the point of DESPOT?

The model, DESPOT, is meant to predict emergent qualitative properties of tree structure and function from the hypothesis that C allocation is regulated to maximize C gain, subject to known biophysical constraints on C gain, resource capture, resource transport and mechanical stability. These predictions can improve our understanding of the constraints and goals from which adaptive properties emerge during tree growth. In the accompanying paper (Buckley and Roberts 2006), we begin working toward this end by evaluating possible reasons for qualitative discrepancies between the model’s predictions and observations. Analysis of the resource relationships predicted by DESPOT might also prove useful in studying the mechanisms of interspecific competition. For example, the “resource-ratio” theory of Tilman (1980, 1982) suggests that a species’ competitive ability is related to its ability to tolerate resource depletion. DESPOT could be used to link familiar tolerance syndromes (e.g., drought tolerance or shade tolerance) to measurable physiological characters. One would construct imaginary species with distinct parameter sets, apply them to DESPOT under varying resource availabilities and catalogue the patterns of tolerance that emerge in the model.

Critically, the model is not meant to be a numerically accurate or predictively useful facsimile of real tree or forest growth. To ensure accuracy by applying ad hoc constraints would be to beg the question by presuming certain outcomes. A more powerful approach is to see what emerges from the optimality hypothesis with minimal constraints and only then to modify the goal and add plausible constraints to bring predictions more in line with observations. In other words, the starting point, or the null hypothesis, should be informed as little as possible by our knowledge or intuition concerning emergent properties of adaptive regulation. “It is not the resemblance between models and reality that lead to new discoveries, but the discrepancies between them” (Pielou 1981) and, “the purpose of models is not to fit the data but to sharpen the questions” (Karlin April 20, 1983; Fisher memorial lecture, Royal Society, London), quoted in Woodward (1987).

Conclusion

The model DESPOT predicts sustained productivity and determine $H$ growth, but rapid early increases followed by slow declines in both ANPP and LAI. Monte Carlo parameter sensitivity analysis shows that most of these predictions are robust to substantial parameter variation. However, of the 100 parameter sets compared in that analysis, about half led to rapid declines in productivity rather than to sustained growth. In the cases where productivity was sustained, the ratios of NPP to GPP and $L$ to $S$ were somewhat conserved among mature, age-matched simulated trees with different parameter sets. In contrast to DESPOT’s predictions, most data show sustained $H$ growth and declining productivity. The accompanying paper (Buckley and Roberts 2006), which uses the model to analyze hydraulic adjustment during $H$ growth in greater detail, discusses possible reasons for these discrepancies.
Acknowledgments
T.N.B. thanks Nathan Phillips and Graham Farquhar for feedback and encouragement; Mike Ryan, Creighton Litton, C.P. Patrick Reid and the USFS Rocky Mountain Research Station Library for providing data to assist with parameter estimation; and Tim Brodribb, David Whitehead, Margaret Barbour, Tom Givnish, Julia Powles, Mike Ryan, Stefan Arndt, Karel Mokany, Mike Roderick and Lawren Sack for helpful input. This work was supported by US National Science Foundation Grant No. 9903947 to DWR, and by the Cooperative Research Centre for Greenhouse Accounting, hosted by the Research School of Biological Sciences at the Australian National University.

References


Ryan, M.G. 1989. Sapwood volume for three subalpine conifers: predictions from structural and physiological metrics and units are given in Tables 1 and 2. Figure A1 is a diagrammatic illustration of key structural metrics and of their use in windthrow risk calculations (see Windthrow risk below).


Appendix

This Appendix describes the DESPOT (Deducing Emergent Structure and Physiology Of Trees) model. Symbols are defined and units are given in Tables 1 and 2. Figure A1 is a diagrammatic illustration of key structural metrics and of their use in windthrow risk calculations (see Windthrow risk below).

Carbon allocation

In each time step, C made available in the previous time step is allocated among three pools (leaf, fine root and sapwood C; where Cref, Cfr, and Csw, respectively) using five allocation fractions—one for leaves (aL), one for fine roots (aR), and three for sapwood: radial or diameter growth (a1), H growth (aH) and depth (i.e., belowground woody tissue) growth (aD):

\[
\begin{align*}
\delta C^+_{\text{leaf}} &= \delta C^+_{\text{fr}} = \delta C^+_{\text{sw}} = \delta C^+_{\text{fr}} = \delta C^+_{\text{sw}} \\
\delta C^+_{\text{fr}} &= \delta C^+_{\text{fr}} = \delta C^+_{\text{fr}} = \delta C^+_{\text{fr}} = \delta C^+_{\text{fr}} \\
\delta C^+_{\text{sw}} &= \delta C^+_{\text{sw}} = \delta C^+_{\text{sw}} = \delta C^+_{\text{sw}} = \delta C^+_{\text{sw}} \\
\delta C^+_{\text{fr}} &= \delta C^+_{\text{fr}} = \delta C^+_{\text{fr}} = \delta C^+_{\text{fr}} = \delta C^+_{\text{fr}} \\
\delta C^+_{\text{sw}} &= \delta C^+_{\text{sw}} = \delta C^+_{\text{sw}} = \delta C^+_{\text{sw}} = \delta C^+_{\text{sw}} \\
\delta C^+_{\text{fr}} &= \delta C^+_{\text{fr}} = \delta C^+_{\text{fr}} = \delta C^+_{\text{fr}} = \delta C^+_{\text{fr}} \\
\delta C^+_{\text{sw}} &= \delta C^+_{\text{sw}} = \delta C^+_{\text{sw}} = \delta C^+_{\text{sw}} = \delta C^+_{\text{sw}} \tag{A1}
\end{align*}
\]

where \( H, Z \) and \( D_0 \) are \( H, \) depth (i.e., effective length of belowground woody tissue, discussed below under Structural metrics) and basal trunk diameter, respectively, \( C_h \) is whole-tree C content and the “+” superscripts distinguish new growth from total increments, which include senescence. Senescence and sapwood–heartwood conversion are described below. In each time step, a numerical algorithm identifies the vector of allocation fractions that maximizes single-tree net C gain (\( A_n \).)
in the next time step. The total growth increment, \( \delta C^* \), is \( A_\nu \delta t \)
where \( \delta t \) is the time step (implicitly 1 year, in the sense that no seasonal effects are considered, but the numerical simulation operates on a much shorter time step of 0.02 years for the sake of stability).

**Carbon gain and respiration**

Single-tree annual net primary production \( (A_s) \) is defined as gross photosynthesis \( (A_c) \) minus maintenance respiration \( (R_m) \), proportional to tissue N contents) and construction respiration (a fixed fraction \( (f_c) \) of \( A_c - R_m \):

\[
A_s = (1 - f_c)(A_c - R_m) =
(1 - f_c)(A_c - v(n_{sw}C_{sw} + n_iC_i + N_c))
\] (A2)

where \( v \) is annual respiration per unit tissue N, \( n_t \) and \( n_{sw} \) are fine root and sapwood N/C ratios and \( N_c \) is total canopy N content. Gross canopy photosynthesis is the product of leaf-level gross photosynthesis and total leaf area \( (L) \), upscaled by a time factor, \( Y \):

\[
A_c = YL(A + R_l)
\] (A3)

where \( A \) and \( R_l \) are leaf-level net CO\(_2\) assimilation and daytime respiration rates, respectively. There are three expressions for \( A \). One describes the rate of CO\(_2\) diffusion through stomata, and is denoted \( A_c \), where \( s = \text{supply-limited} \):

\[
A_s = g_{sw}(c_a - c_i)
\] (A4)

where \( g_{sw} \) is total conductance to CO\(_2\) and \( c_a \) and \( c_i \) are ambient and intercellular CO\(_2\) mole fractions, respectively. When \( A \) is limited by CO\(_2\) demand, it approaches the lesser of two values, \( A_s \) and \( A_r \), representing RuBP carboxylation and regeneration-limited rates, respectively. \( A_s \) and \( A_r \) are given by Farquhar et al. (1980) as:

\[
A_s = \frac{V_m(c_i - G_r)}{c_i + K^*} - R_l \quad A_r = \frac{J(c_i) - G_r}{4(c_i + 2G_r)} - R_l
\] (A5)

where \( V_m \) is maximum velocity and \( K^* \) is effective Michaelis constant for RuBP carboxylation, \( G_r \) is the photorespiratory compensation point, \( R_l \) is daytime leaf respiration rate and \( J \) is potential electron transport rate. Both \( G_r \) and \( K^* \) are treated as constants; \( V_m \) and \( J \) are discussed below. Determination of \( A \) involves first solving \( A_c \) with each of \( A_s \) and \( A_r \) to constrain \( c_i \) and thereby remove it from the equations, and then by calculating the hyperbolic minimum of the two resulting values of \( A \) (denoted \( A_c \cap A_r \) and \( A_r \cap A_s \)):

\[
A = \min \{A_c \cap A_r, A_r \cap A_s, \theta_A \}
\] (A6)

where "\( \min \{x, y, z\} \)" is shorthand for "the lesser solution \( Q \) of \( zQ^2 - (x + y)Q + xy = 0 \)."

**Resource dependence of photosynthetic parameters**

Leaf-level transpiration rate \( (E) \), nitrogen content \( (N) \) and incident photosynthetic irradiance \( (I) \) influence \( g_{sw}, V_m, J \) and \( R_l \) as follows. The value of \( J \) is calculated as \( \min \{J_m, \phi J, \theta_J \} \) (Farquhar and Wong 1984); \( \phi \) and \( \theta_J \) are constants and \( J_m = \chi N_c, V_m \) is assumed proportional to \( J_m \) as \( V_m = J_m/2.1 \) (Wullschleger 1993), and \( R_l \) is assumed proportional to \( V_m \) as \( R_l = 0.01V_m \) (de Pury and Farquhar 1997). The value of \( g_{sw} \) is given by \( g_{sw}(1.6 + 1.37 \cdot r_{sw}g_{sw}) \), where \( g_{sw} \) and \( r_{sw} \) are stomatal conductance and boundary layer resistance to water vapor, respectively, and \( g_{sw} = E/(D - r_{sw}E) \), where \( D \) is leaf-to-air water vapor mole fraction gradient. The leaf-level model for \( A \) is assumed scale-invariant (i.e., the canopy is a "big-leaf"), so it is driven by canopy averages for \( N, I \) and \( E \): \( N = N/I, I = I/L \) and \( E = E/L \), where \( L \) is total leaf area, \( N_c \) is canopy photosynthetic N content, \( E_c \) is whole-tree transpiration rate, and \( I_c \) is canopy absorbed photosynthetic irradiance. The next section describes how \( E_c, N_c \) and \( I_c \) are calculated.

**Photosynthetic resource capture and delivery**

Stomatal conductance is calculated from leaf transpiration rate:

\[
g_{sw} = E/(D - r_{sw}E) = E/L/(D - r_{sw}E/L).
\]

In turn, \( E_c \) is calculated by assuming canopy transpiration occurs in steady-state with uptake by roots and axial flow through coarse roots and the trunk, according to Darcy’s Law:

\[
E_c = \frac{\Delta P}{r_s + r_r + r_i} = \frac{\Psi_c - \Psi_l - \rho g h}{(k_{sw}C_i)^4} + \frac{\eta V_m}{k_s S} + \frac{r_{sw}}{L}
\] (A7)

where \( \rho \) is water density and \( g \) is gravitational acceleration. Vertical distance to the center of the canopy, \( h \) (Figure A1c), is \( H(1 - 0.5 \cdot \text{LCR}) + Z(1/2) \) (assumed coarse roots are at a 45° angle), axial flow path length, \( l \) (Figure A1b), is \( H(1 - 0.5 \cdot \text{LCR}) + Z + 0.5G^{0.5} \) (the last term represents lateral flow parallel to the ground, where \( G \) is the ground area subtended by the canopy, or the square of canopy width). Sapwood permeability is \( k_{sw} \), \( \eta \) is dynamic viscosity of water \((1.0 \times 10^{-3} \text{ MPa s at } 20^\circ C) \) and \( V_m \) is molar volume of water \((18 \times 10^{-6} \text{ m}^3 \text{ mol}^{-1}) \). The laminar resistance and total surface area of a single leaf are assumed constant, so \( r_{sw} \) is also a constant. Soil water potential, \( (\Psi_c) \), is treated as a constant. In the present paper, leaf water potential \( (\Psi_l) \) is also assumed constant, representing an isohydric state adapted to keep xylem tension above some threshold. The accompanying paper (Buckley and Roberts 2006) relaxes the isohydric assumption to study the effect of dynamic compensation mechanisms (increased sapwood permeability or reduced \( \Psi_l \) with \( H \)) and the costs of associated increases in embolism risk.

The total amount of N contained in leaves, \( (N_c) \), is simulated dynamically as the balance between N sources (uptake by fine roots and inputs of recycled N from senescing tissues) and N sinks other than new leaves (losses due to leaf senescence and N requirements of new fine roots and sapwood). Following Dewar and McMurtrie (1996), we assume N uptake is a fraction of the total rate of inputs into the soil and that the fraction
increases in saturating fashion with fine root C per unit ground area \((C_r/G)\). Then, if N inputs occur at a rate of \(U_o\) per unit ground area, the rate of N uptake is:

\[
U = (GU_o) \frac{C_r}{C_r + \kappa G}
\]

where \(\kappa\) is fine root C per ground area at which uptake equals half the input rate. The finite increment in \(N_t\) in one time step is then given by:

\[
\delta N_t = \left( (U + \gamma n_1 \delta C_i^- + \gamma_i n_{sw} \delta C_{sw}) - (n_1 \delta C_i^- + n_i \delta C_i^+ + n_{sw} \delta C_{sw}) \right) \delta_t
\]

where \(\lambda_i\) and \(\lambda_{sw}\) are leaf and sapwood N recycling fractions; \(\delta C_i^-\) and \(\delta C_{sw}\) are senescence losses of leaf and sapwood C in the current time step; and \(n_1\) (leaf N/C ratio) is shorthand for \(N_t/C_i\).

Light capture \((I_i)\) is estimated by analogy to the Beer-Lambert Law. For a laterally uniform canopy with spherical leaf angle distribution and uniform spatial distribution of leaf area, \(I_i\) may be approximated as:

\[
I_i = GI_s \cos(1 - e^{-k_i L_{sec}})
\]

where \(k_i\) is the incoming irradiance on a surface normal to the solar beam and \(L_{sec}\) is the solar elevation below the zenith (Figure A2). This does not, however, predict the increase in light capture resulting from vertical growth that puts some of a tree’s canopy above its neighbors. In that case, the change in \(I_i\) can be estimated by integrating along each of a series of parallel solar paths, some of which are attenuated by adjacent trees before reaching the “target” tree (Figure A2). Light capture is then equal to \(\alpha_i G \lambda_s\), where canopy absorptance, \(\alpha_i\), is:

\[
\alpha_i = G^{-0.5} \int_0^{\theta_p} \sin^{-1} \left(1 - e^{-k_i L_{sec}}\right) dx
\]

Figure A2. Estimated versus measured aboveground woody carbon, based on measurements of biomass, height \((H)\) and basal diameter (or DBH corrected to basal diameter) made by Reid et al. (1974) (open symbols) and Litton (2002) (closed symbols) for lodgepole pine trees in stands of varying nutrient status and stand densities. The parameter \(\xi\) was chosen to produce the best fit. The 1:1 line is shown for comparison. Abbreviations: \(p_{cw}\) = wood carbon density; and \(D_b\) = basal trunk diameter.
where \( k = k_L A_{LAI}/h \) is an effective extinction coefficient relative to path length, \( h \) is canopy depth (LCR-H) and \( p_0(x) \) and \( p_\beta(x) \) are the path lengths through the target tree and neighboring trees, respectively, expressed as functions of the horizontal position of each path’s intersection with the top of the canopy (Figure A2). It can be shown that this integral evaluates to two different expressions, depending on \( \beta \). For low \( \beta \) (sun high in the sky) or short or broad trees (\( \beta < \arctan(\sqrt{G}/h) \), Figure A2):

\[
\alpha_c = \alpha^* \cos \beta + G^{0.5} \alpha^*
\]

\[
(\alpha^* k^{-1} \cos \beta \sin \beta - (h - \delta H) \sin \beta e^{-(h - \delta H) \cos \beta})
\]

(When \( \delta H = 0 \), both expressions for \( \alpha_c \) collapse to \( \cos \beta (1 - e^{-kL_{sec}\beta}) \)). This formulation is incorrect before canopy closure, because it does not account for open space between adjacent trees. However, although the error overestimates the benefit of \( H \) growth before closure, the model predicts negligible \( H \) growth before canopy closure, so the effect of the error is also negligible.

**Structural metrics**

We assume total stem volume is proportional to the product of basal area and the sum of \( H, Z \) and \( W = G^{1/2} \) (crown width), thus:

\[
\text{stem volume} = \xi D_b^2 (H + Z + W) = \rho_{sw} D_b^2 C_w
\]

where \( D_b \) is basal trunk diameter, \( C_w = C_{sw} + C_{bw} \), \( \rho_{sw} \) is wood C density and \( \xi \) is an empirical parameter relating linear dimensions to wood volume. Although tapering and branching are not explicitly described, \( \xi \) implicitly captures the aspects of tapering and branching relevant to DESPOT. The value of \( \xi \) used in these simulations (0.299) corresponds to an aboveground woody branching network with about 50% more volume than a single stem of length \( H \) and standard –3/2-law taper; this value was found to describe aboveground woody allometry for lodgepole pine across a broad range of tree sizes (Figure A3; see Parameter estimation for more details). Positive increments in stem C occur only by sapwood production, so \( \delta C_w^* = \delta C_w \) when calculating allocation. To calculate increments in \( D_b, S, H \) and \( Z \) given a total available C increment (\( \delta C_t \)), the first step is to deduce from \( \delta C_t \) the cost in stem C of lateral canopy extension to cover ground area freed up by stand thinning. This is done by calculating the change in ground area and thus in \( W (\delta W) \) caused by thinning, from \( \delta C_t \) and the self-thinning equation (Equation A21) and then calculating the increment in \( C_{sw} \) needed to produce lateral stem extension of \( \delta W \), from the product of \( \delta W \) and the sensitivity of \( C_w \) to \( W \):

\[
\delta C_w^* = \delta C_t - \delta W \left( \frac{\partial C_w}{\partial W} \right) = \delta C_t - \delta W \cdot \xi \rho_{sw} D_b^2
\]

The total C increment available for allocation, \( \delta C_t^* \), is then partitioned in similar fashion to calculate increments in \( D_b, H \) and \( Z \):

\[
\delta H = a_i \delta C_t^* \left( \frac{\partial H}{\partial C_w} \right) = a_i \delta C_t^* \xi \rho_{bw} D_b^2
\]

\[
\delta Z = a_i \delta C_t^* \left( \frac{\partial Z}{\partial C_w} \right) = a_i \delta C_t^* \xi \rho_{bw} D_b^2
\]

\[
\delta D_b = a_i \delta C_t^* \left( \frac{\partial D_b}{\partial C_w} \right) = \frac{a_i \delta C_t^*}{2 \xi \rho_{bw} D_b (H + Z + W)}
\]
Senescence and heartwood conversion

The processes that determine senescence rates and sapwood to heartwood conversion are not well understood, so we simulate senescence empirically. Each time step’s new increment in leaf, fine root and sapwood C is tracked over time and a portion of that increment is deducted in each subsequent time step, based on the increment’s age. We found sapwood lifespan distributions in lodgepole pine trees from northwestern Wyoming obeyed a Weibull lifespan distribution with median lifespan 14 years (see Parameter estimation); the failure rate (the probability of a randomly chosen increment failing, i.e., senescing) for this type of distribution is $\varepsilon(\text{age/lifespan})^{-1}$, where $\varepsilon$ is a dimensionless parameter. We assumed that leaf and fine root increments had senescence dynamics qualitatively similar to those of sapwood, but with different median lifespans ($\tau_1$ and $\tau_r$, respectively).

Thus, in each time step $t \rightarrow t + \delta t$, the increment $\delta C_x^r$ produced at each earlier time $T$ (where the subscript $x$ represents $sw$, $l$ or $r$, for sapwood, leaves and fine roots, respectively) is decremented such that what remains of the original increment in the next time step, $\delta C_x^r(T; t + \delta t)$, is given by Equation A18:

$$\delta C_x^r(T; t + \delta t) = \delta C_x^r(T_t) - \delta t \varepsilon \left(\frac{t - T}{\tau_x}\right)^{\tau_x-1}$$  (A18)

where the $\tau_x$ are tissue-specific median lifespans ($\tau_s$, $\tau_l$, or $\tau_r$). The new value of $C_x$ is then calculated by summing the surviving remainders of all previous increments and adding the current time step’s new increments (Equation A19):

$$C_x(t + \delta t) = \sum_{T=0}^{t} \delta C_x^r(T; t + \delta t) + a_x(t + \delta t)\delta C_x^r$$  (A19)

For sapwood, $a_x = a_h + a_d + a_s$, and the C increment due to lateral crown expansion, calculated from Equation A14, is added to the value of $C_{sw}$ calculated by Equation A19. Heartwood C ($C_{hw}$) is incremented in each time step by the amount of sapwood C lost in that time step, which is given by $C_{sw}(t)$ minus the term in square brackets on the right-hand-side of Equation A19. Sapwood area ($S$) was calculated from $C_{sw}$ assuming the sapwood/heartwood area fraction was uniform throughout the tree, so that sapwood volume is $S(H + Z + W)$ and:

$$S = \frac{C_{sw}}{\rho \varepsilon \rho_{sw}(H + Z + W)}$$  (A20)

Stand and environment

Although DESPOT is an individual-tree model, some information about stand properties is required to complete the simulation; for simplicity, we assume the stand consists of identical, evenly spaced trees, and that density-dependent mortality causes stand density ($\rho_s$) to vary with the $-2/3$ power of single tree biomass (proportional to total):

$$\rho_s = \rho_s C_t^{\frac{2}{3}}$$  (A21)

Penalizing windthrow risk

The model outlined above produces a continuous relationship between allocation parameters and C gain, so it appears economically self-contained. However, it does not impose a cost on windthrow risk, because windthrow does not affect C balance until it causes mortality. We costed tree geometry with respect to windthrow risk by modulating allocation to maximize expected net C gain, based on the probability that a certain tree geometry will fail in severe winds.

The tree will break or uproot if the wind drag ($T_u$, the turning moment imposed on the stem by wind) exceeds either the bending moment causing stem breakage ($T_b$) or the turning moment causing uprooting ($T_u$). These moments may be approximated as follows. Wind at speed $v$ applies a force proportional to $v^2$ on the canopy, whose “sail area” in calm air is $W(LCRH)$ ($W = G^{1.3}$ is crown width); supposing the vertical center of this sail is anchored to the stem, the lever arm is $H(1 - 0.5LCR)$. However, canopy streamlining reduces the effective sail area as wind speed rises, such that drag increases roughly linearly with $v$, rather than $v^2$ (Mayhead 1973). Hence, we may write $T_u \propto vW^2LCR(1 - 0.5LCR)$ (Figure A1d). The critical bending moment causing stem breakage, $T_b$, is proportional to the cube of basal diameter, $D_b^3$ (e.g., Jones 1992, Peltola et al. 1999, Gardiner et al. 2000). The HWIND model (Peltola et al. 1999) assumes resistive moment for uprooting is proportional to the mass of the root:soil plate, with lever arm equal to depth of the root:soil plate. We assume the root system occupies a hemispherical volume of radius $Z$ (rooting depth), and that its density is constant so its mass scales isometrically with its volume ($Z^3$). Hence $T_u \propto Z(Z^3)$ (Figure A1e). Equating $T_u$ with $T_b$ and $T_u$ yields:

$$V_b = \frac{w_b D_b^3}{xWH^2}$$  (A22)

$$V_u = \frac{w_u Z^4}{xWH^2}$$  (A23)
reverse Weibull distribution (Simiu et al. 2001, Dougherty et al. 2003), so the probability $p_1$ that an observation $V_i$ exceeds some value $V^*$ (where $x$ is shorthand for either $b$ or $a$, representing breakage and uprooting, respectively) is

$$p_1 = p(V_i > V^*) = (1 + \omega V_i)^{-1}$$

(A24)

To apply these windthrow risk calculations to our simulations, $A_n$ first was calculated without consideration of mechanical stability for each C allocation vector in each time step. Then, Equations A22–A24 were used to calculate the annual probabilities of breakage and uprooting, given the values of $D$, $H$, $Z$ and $G$ that would result in the next time step from each candidate allocation vector. Finally, $A_n$ was multiplied by the complement of the larger of these two probabilities. The net effect of this procedure is to penalize mechanically risky tree geometries, to make them appear less profitable to the optimization algorithm. Estimation of the parameters $w_b$, $w_a$ and $\omega$ is described under Parameter estimation.

Numerical optimization procedures

In each time step, C allocation vectors (sets of C allocation fractions, $a_s$, $a_t$, $a_g$, $a_d$, and $a_z$, that sum to unity) that maximized $A_n$ in the subsequent time step were identified using a genetic algorithm having the following procedure: (1) $n\times m$ vectors were generated randomly. (2) $A_n$ was calculated for each vector. (3) The $m$ highest-scoring vectors were identified. (4) Then $n$ new vectors were generated from each of the $m$ winners by mutating the winners’ original components (say $a_t$), by choosing new components randomly in the range $a_t(1 \pm B)$ and renormalizing the resulting vectors. (5) Steps 2–4 were repeated until the square of the relative difference in $A_n$ between the best and the $m$th best vectors was less than some threshold, $\delta$. To ensure continued improvement between cycles, $B$ was reduced exponentially in successive cycles. In the simulations presented here and in the accompanying paper (Buckley and Roberts 2006), the numerical values of $n$, $m$, $\delta$ and $B$ were 500, 4, 10$^{-15}$ and 0.5, respectively.

A Nelder-Mead simplex technique worked on simpler versions of this model; we tried a simplex and numerous other hill-climbing and conjugate gradient techniques on DESPOT, but none proved sufficiently robust, even when the search routine was performed in an edgeless space transformed from the hyperplane segment comprising allowable allocation vectors. For any technique to work, we found it necessary to remove all thresholds or slope discontinuities in the model’s mathematical structure by hyperbolic minimization or maximization.

Parameter estimation

Most values in the standard parameter set given in Table 2 were estimated for the 40-year-old lodgepole pine stand studied initially by Ryan and Waring (1992) (RW) and later by Yoder et al. (1994) and Murty et al. (1996) (MMR). Parameters that could not be estimated on that basis were taken from the literature or derived from our own measurements of pure lodgepole pine stands in the Shoshone National Forest of Wyoming, USA, in 2000 and 2001.

Parameters taken directly from MMR or RW include leaf and sapwood N recycling efficiencies ($\gamma_l$ and $\gamma_{sw}$, 0.5 and 0.6); median leaf and fine root lifespans ($\tau_l$ and $\tau_r$, 8.3 and 1 years); N content of new sapwood ($n_{sw}$, 1.2 mmol N (mol C)$^{-1}$); canopy light extinction coefficient ($k_L$, 0.5 m$^{-1}$); leaf area per unit leaf C (SLA, 0.091 m$^2$ (mol C)$^{-1}$); construction respiration fraction ($\chi_f$, 0.22, based on 28% of NPP; RW); self-thinning parameter ($\rho_{sw}$, 49 stems m$^{-2}$ (mol C)$^{-1}$; estimated by fitting the self-thinning curve to biomass and stand density data from RW). The following parameters were taken directly from other sources: fine root N:C ratio, $n_r = 17$mmol N (mol C)$^{-1}$ (Dewar and McMurtrie 1996); N cost of electron transport capacity, $\chi_t = 1.9 \mu$mol e$^{-}$ (mmol N)$^{-1}$ s$^{-1}$ (de Pury and Farquhar 1997); annual maintenance respiration per unit tissue (v, 0.041 mol C mmol$^{-1}$ N year$^{-1}$ (Ryan 1991); wood C density, $\rho_{cw}$, 1.4 $\times$ 10$^4$ mol C m$^{-3}$, assuming wood is 40% C by mass (Ryan 1989); sapwood permeability, $k_s$, 2.05 $\times$ 10$^{-12}$ m$^2$ (Whitehead et al. 1984, for lodgepole pine); and soil and leaf water potential, $\Psi_s$, $\Psi_l$, = –0.5 and –1.5 MPa (estimated from predawn and midday values given by Yoder et al. 1994 for the 400-year-old RW stand). Laminar resistance ($r_l = 60$ MPa s (mol H$_2$O)$^{-1}$) was estimated arbitrarily from the low end of the range of values (59–258) found in the literature for broadleaved species (Sack et al. 2002, Nardini et al. 2003, Sack et al. 2004).

The relationship between linear trunk dimensions ($D_h$, $H$ and $Z$) and total woody tissue volume ($\xi = 0.299$ m$^3$; Equation A13) was estimated from allometric data for lodgepole pine (Reid et al. 1974, Litton 2002), from stands with densities ranging from 475–75,500 stems ha$^{-1}$ (plus one plot with nearly 600,000 stems ha$^{-1}$), with trees of $D_h$ and $H$ ranging from 1–32 cm and 0.6–17.5 m, respectively. Figure A3 shows $\rho_{sw}$, $\xi D_h^3 H$ versus $C_s$ for all of these data, using our values of $\xi$ and $\rho_{sw}$, and assuming woody biomass was 40% C. This value of $\xi$ corresponds to a branching system where the total volume of aboveground stems and branches is 38% of the volume of a cylinder with basal diameter $D_h$ and length $H$, or a self-similar, space-filling branching network of length $H$ (both of which have volume = $\pi D_h^2 H/4$): 0.299$D_h^2 H = 0.38$ ($\pi D_h^2 H/4$). This is roughly 50% more volume than a stem with standard 3/2-law taper (where volume = $\pi D_h^2 H/16$).

Soil-to-xylem hydraulic conductance per unit fine root C ($k_m = 6.6 \times 10^{-4}$ mol H$_2$O MPa$^{-1}$ s$^{-1}$ (mol$^{-1}$C)) was estimated by assuming, arbitrarily, that half the total hydraulic resistance in the 40-year-old RW lodgepole stand occurred in the soil and fine roots; values for axial and total laminar resistance were calculated from $H$, leaf area and sapwood area in that stand, given our estimates for $r_l$ and $k_s$ and assuming belowground axial path was 0.32$H$ (from the average ratio of above- to belowground woody biomass in Scots pine and Norway spruce given by Gardiner et al. 2000); those data were also used to estimate windthrow risk parameters below). Nitrogen input ($U_n = 660$ mmol N m$^{-2}$ year$^{-1}$) and fine root per ground
area at half uptake saturation ($\kappa = 16 \text{ mol C m}^{-2}$) were estimated assuming N uptake and losses were balanced and uptake was half-saturated in the 40-year-old RW stands.

Median sapwood lifespan ($\tau_s = 14$ years) was estimated from the observed frequency distribution of sapwood lifespans (number of sapwood rings) in 317 lodgepole pine trees from 62 plots in the Shoshone NF, Wyoming in 2001. The number of sapwood rings was calculated from hand measurements of sapwood radius and automated measurements of ring widths on two cores from opposite quadrants of each tree. Live crown ratio (LCR = 0.84) was the average from 27 lodgepole pine trees observed in the Shoshone in 2000 and 2001.

The extreme value index for windspeed frequencies, $\omega$, was taken as $-0.25$, an approximate value for several Pacific Northwest sites from Dougherty et al. (2003). Values of $w_b$ and $w_u$ were estimated as $1.15 \times 10^5$ and 2.3 m$^{-1}$, respectively; these are average values calculated from data on Scots pine and Norway spruce used by Gardiner et al. (2000) to test the HWIND and GALES models, assuming those observed tree geometries were on the cusp of nonzero probability of damage ($V = -1/\omega = 4$; Equations A22–A24). Boundary layer resistance to water vapor ($r_{bw} = 0.5 \text{ mol}^{-1} \text{ m}^2 \text{ s}$), leaf-to-air water vapor mole fraction gradient ($D = 0.015 \text{ mol H}_2\text{O mol}^{-1}$), quantum yield of electrons from incident irradiance ($\phi = 0.3 \text{ e}^{-}\text{ photon}^{-1}$), and initial stand density ($\rho_{si} = 5.0 \text{ stems m}^{-2}$ (5000 stems ha$^{-1}$)) were chosen arbitrarily.

Solar beam irradiance ($I_s = 1915 \mu\text{mol m}^{-2} \text{ s}^{-1}$) and effective mean solar angle below the zenith ($\beta = 54.5^\circ$) were calculated as follows. Incident irradiance on a level surface above the canopy was calculated 20 times in each of 90 days (3 month growing season, June–August), at a latitude of 40° N for the RW sites (using equations given by de Pury and Farquhar 1997), and $I_s$ was adjusted to yield the total growing season PAR given by MMR (converted to photon flux basis assuming $\lambda = 550 \text{ nm}$). Effective mean solar angle was then calculated as the arccosine of the ratio of mean level-surface irradiance over the growing season to $I_s$.

Total C gain is overestimated when assimilation is extrapolated from the value calculated at a mean irradiance, because assimilation responds to light in saturating fashion. This non-linear averaging error was corrected by assuming the response of canopy assimilation to irradiance, like that of leaf-level electron transport and assimilation, is described by a non-rectangular hyperbola or “hyperbolic minimum,” and by multiplying the number of seconds of daylight in the growing season by the average value (0.67) of the ratio of the hyperbolic minima of actual and mean irradiance over the growing season, using the same convexity parameter (0.90) as for leaf-level $J$ and $A$. This yields $3.1 \times 10^6 \text{ s year}^{-1}$ ($0.67 \times 90 \text{ days} \times 14.3 \text{h} \times 3600 \text{s}$, where 14.3 h = mean daylength), and hence $Y = 3.1 \text{ mol year}^{-1} (\mu\text{mol s}^{-1})^{-1}$. 
