A modeling framework for inferring tree growth and allocation from physiological, morphological and allometric traits

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Summary Predictions of forest succession, diversity and function require an understanding of how species differ in their growth, allocation patterns and susceptibility to mortality. These processes in turn are affected by allometric constraints and the physiological state of the tree, both of which are coupled to the tree’s labile carbon status. Ultimately, insight into the hidden labile pools and the processes affecting the allocation of labile carbon to storage, maintenance and growth will improve our ability to predict tree growth, mortality and forest dynamics. We developed the ‘Allometrically Constrained Growth and Carbon Allocation’ (ACGCA) model that explicitly couples tree growth, mortality, allometries and labile carbon. This coupling results in (1) a semi-mechanistic basis for predicting tree death, (2) an allocation scheme that simultaneously satisfies allometric relationships and physiology-based carbon dynamics and (3) a range of physiological states that are consistent with tree behavior (e.g., healthy, static, shrinking, recovering, recovered and dead). We present the ACGCA model and illustrate aspects of its behavior by conducting simulations under different forest gap dynamics scenarios and with parameter values obtained for two ecologically dissimilar species: loblolly pine (\textit{Pinus taeda} L.) and red maple (\textit{Acer rubrum} L.). The model reproduces growth and mortality patterns of these species that are consistent with their shade-tolerance and succession status. The ACGCA framework provides an alternative, and potentially improved, approach for predicting tree growth, mortality and forest dynamics.

Keywords: \textit{Acer rubrum}, carbon allocation, carbon reserves, carbon storage, growth model, labile carbon, loblolly pine, \textit{Pinus taeda}, red maple, retranslocation, shade-tolerance, succession, tree mortality.

Introduction

Understanding and predicting tree growth, carbon allocation and mortality have been a longstanding challenge. A biologically consistent representation of these processes is paramount to predict the potential effects of climate change on forest structure, productivity and biodiversity (Loehle and LeBlanc 1996, Norby et al. 2001). Numerous tree growth models (see reviews by Hawkes 2000, Le Roux et al. 2001), allocation schemes (see Ågren and Wikström 1993, Cannell and Dewar 1994, Lacointe 2000) and mortality algorithms (see Hawkes 2000, Keane et al. 2001) have been developed. There is room for improvement, however, in linking these key processes within a mechanistic framework that is capable of reproducing observed tree growth and forest dynamics (e.g., Schenk 1996, Hawkes 2000).

Two popular approaches for modeling tree growth attack the problem from different angles. For example, many models employ an allometric foundation that ranges from fairly simple scaling rules (e.g., Thomas 1996, Enquist et al. 1999, Niklas and Enquist 2002\textsuperscript{b}, Niklas 2004) to more detailed formulations that couple allometries and basic biomass production equations (e.g., Kohyama 1991, Bartelink 1998, see review by Bugmann 2001). In general, these models are highly empirical, which may be an attractive quality because they can usually be parameterized with field data (e.g., Valentine and Mäkelä 2005). An alternative modeling approach is grounded in physiology; these models range from empirical representations of carbon dynamics (Bossel 1986, Dewar 1997) to semi-mechanistic models of carbon gain, loss and allocation (e.g., Weinstein et al. 1991, Bossel 1996, Landsberg and Waring 1997). Although allometric models consider only structural carbon (biomass), most physiology models describe structural and transient (e.g., recent photosynthates) carbon, but only a few follow labile carbon reserves (see reviews by Hawkes 2000, Le Roux et al. 2001).

Why is it important to consider both allometric (e.g., structural) traits and physiological processes (including labile carbon) in models of tree growth? First, species vary in their allometries (e.g., Obrien et al. 1995, Thomas 1996, Kohyama et al. 2003), and such species differences potentially contribute to patterns of forest diversity (Kohyama et al. 2003, Poorter et al. 2003) and succession (Fulster and Westoby 1998). Additionally, intra-specific variation in allometries (e.g., Coomes and Grubb 1998) is likely coupled to the physiological state...
of the trees. For example, Kaufmann and Watkins (1990) found that high-vigor (healthy) lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) trees had deeper crowns and higher leaf areas but similar height versus diameter allometries compared to low-vigor trees (see also Kaufmann 1996). It is likely that such changes in a tree’s allometry and health are related to the status of its labile carbon reserves (e.g., Renaud and Mauffette 1991, Coomes and Grubb 1998).

An understanding of labile carbon, especially in terms of storage and retranslocation, appears central to explaining species differences in growth and mortality responses to stress such as low light (Chapin et al. 1990, Niinemets 1998, Canham et al. 1999, Kaelke et al. 2001). Most models of tree growth and forest dynamics, however, do not explicitly link mortality to carbon starvation (see reviews by Loehle and LeBlanc 1996, Hawkes 2000, Keane et al. 2001). Popular approaches employ empirical relationships between the timing (or probability) of tree death and growth trends such as radial increment (e.g., Kobe et al. 1995, Ogle et al. 2000, Wyckoff and Clark 2000, Bigler and Bugmann 2004, Kunstler et al. 2005) or tree age (see Hawkes 2000, Keane et al. 2001). Most tree growth models lack a mechanistic basis for mortality (Loehle and LeBlanc 1996, Hawkes 2000), and only four of the 61 models reviewed by Hawkes (2000) used the balance between carbon demand and supply to predict tree death (Bossel 1986, Weinstein et al. 1991, Bugmann et al. 1997, Friend et al. 1997). These models, however, tend to yield unrealistic mortality rates (Hawkes 2000), which could be explained by the lack of allometric constraints on labile carbon behavior.

A modeling framework that incorporates intrinsic biological processes affecting tree growth, health and mortality is needed (Loehle and LeBlanc 1996, Hawkes 2000). Hence, we developed the ‘Allometrically Constrained Growth and Carbon Allocation’ (hereafter, ACGCA) model. The ACGCA model incorporates empirically-supported allometric constraints on dynamic allocation of carbon, including the critical labile pool that largely determines differences in species’ ecological strategies. We describe the ACGCA model and illustrate important aspects of its behavior by conducting simulations with parameters derived for two species common to the eastern United States: loblolly pine (*Pinus taeda* L.) and red maple (*Acer rubrum* L.). Currently, light is the only environmental driver, and we use the ACGCA model to simulate growth, labile carbon (e.g., allocation) and mortality patterns of these species under different light regimes representative of forest canopy gap formation and closure. In doing so, we find that the model captures a range of behaviors that are consistent with what we know about the natural history of these two species.

### Conceptual overview

The ACGCA model is capable of reproducing a range of physiological states that are defined by a tree’s allometric and labile carbon status. The model explicitly considers labile and structural carbon separately, and it is unique because labile carbon allocation and retranslocation are solved so that growth (biomass production) and shrinkage (tissue loss) are consistent with observed allometries. The separation of the carbon pools allows for labile carbon depletion (or starvation) as a mechanism for predicting mortality.

In the ACGCA model, a tree grows or shrinks according to two different allometries, and the transition between the allometries depends on labile carbon status. The allometries describe empirical relationships between the size and the shape of different compartments. Examples include functions that relate tree height to trunk radius and leaf area to sapwood area. We consider a single target allometry that is typical of a healthy, growing tree. Under this allometry, all compartments (i.e., leaves, fine roots, branch and root sapwood, branch and root heartwood, trunk sapwood and trunk heartwood) are in allometric proportion to each other, and each compartment is directly tied to trunk radius. We also consider a flexible reduced allometry for trees that have departed from the target allometry because of a period of negative carbon balance. As a tree starves, it drops nontrunk tissues according to a subset of rules that govern the size and the shape of these compartments, which are no longer related to the trunk because the trunk does not shrink in its mass or dimensions.

The ACGCA model captures six physiological states: healthy, static, shrinking, recovering, recovered and dead (Figure 1). We describe these states based on the model results obtained under the forest gap cycle as shown in Figure 2. Under the initial high-light (open gap) conditions the tree has excess labile carbon because photosynthetic inputs exceed maintenance demands. The excess carbon is allocated to structural growth and labile carbon storage, resulting in a healthy tree that is growing according to the target allometry (Figure 2A). Upon experiencing gradual reductions in light (canopy closure), photosynthesis drops below the level required to satisfy maintenance respiration, and the tree uses labile carbon in the sapwood and senescing tissues to meet these demands and to rebuild senesced leaves, roots and branches (Figure 2B). Thus, the tree is in

![Figure 1](https://academic.oup.com/treephys/article-abstract/29/4/587/1642683/633)

**Figure 1.** The six different physiological states (boxes) described by the ACGCA model and all possible transitions between states (arrows with circled numbers). Each state is associated with either the target or the reduced allometry; transitions depend on the tree’s labile carbon and allometric status.
a static state because it does not change in size or structural mass (see transition 1, Figure 1). Once the tree has depleted its sapwood reserves, it can no longer replace senesced tissues; at this point, the tree is in a shrinking state (transition 2a, Figure 1), and it starts dropping additional (nontrunk) tissues, beyond normal senescence (Figure 2C). The tree shrinks according to the reduced allometry, and the labile carbon that was stored in the dropped tissues is retranslocated to fulfill maintenance demands.

A tree cannot remain in the shrinking state, and there are three possible physiological states that follow (Figure 1). If the tree is stressed for an extended period, it will eventually deplete its stored labile carbon, resulting in tree death (transition 3c, Figure 1). An alternative path is illustrated in Figure 2; stress is alleviated upon creation of the second canopy gap, exposing the tree to high light, stimulating photosynthesis, and thus resulting in excess labile carbon that is allocated to growth and storage. The tree shrinks according to the reduced allometry, and the labile carbon that was stored in the dropped tissues is retranslocated to fulfill maintenance demands.

The ACGCA model

Here, we provide a more detailed overview of the ACGCA model. The model consists of five principal modules: (i) structural carbon, (ii) labile carbon, (iii) allometries, (iv) physiology and (v) allocation and retranslocation. State variables, parameters, auxiliary variables and units are given in Tables 1–3; for ease of presentation, units are typically suppressed in the text. The ACGCA model is currently designed to predict the annual growth of an individual tree. Below, we describe the five modules, primarily in the context of a healthy tree. The Online Supplementary Data document the ACGCA model for all six physiological states.

Note that the ACGCA model is actually much simpler than it may initially appear. Many of the relationships in the different modules describe basic mass balance requirements (carbon modules), some rely on structural assumptions (allometry module), others require assumptions about the physiological drivers (physiology module), and some quantities are constrained by other relationships.

Table 1. State variables in the ACGCA model, describing the state of an individual tree.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>B_L</td>
<td>Biomass of leaves</td>
<td>g dw</td>
</tr>
<tr>
<td>B_O</td>
<td>Biomass of other wood</td>
<td>g dw</td>
</tr>
<tr>
<td></td>
<td>(coarse roots and branches)</td>
<td></td>
</tr>
<tr>
<td>B_OH</td>
<td>Biomass of other heartwood</td>
<td>g dw</td>
</tr>
<tr>
<td>B_OS</td>
<td>Biomass of other sapwood</td>
<td>g dw</td>
</tr>
<tr>
<td>B_R</td>
<td>Biomass of roots</td>
<td>g dw</td>
</tr>
<tr>
<td>B_S</td>
<td>Biomass of sapwood</td>
<td>g dw</td>
</tr>
<tr>
<td></td>
<td>(trunk, coarse roots and branches)</td>
<td></td>
</tr>
<tr>
<td>B_T</td>
<td>Biomass of trunk</td>
<td>g dw</td>
</tr>
<tr>
<td>B_TH</td>
<td>Biomass of trunk heartwood</td>
<td>g dw</td>
</tr>
<tr>
<td>B_TS</td>
<td>Biomass of trunk sapwood</td>
<td>g dw</td>
</tr>
<tr>
<td>C_LR</td>
<td>Labile carbon in leaves and fine roots</td>
<td>g gluc</td>
</tr>
<tr>
<td>C_S</td>
<td>Labile carbon in sapwood</td>
<td>g gluc</td>
</tr>
<tr>
<td>r</td>
<td>Trunk radius at base of tree</td>
<td>m</td>
</tr>
</tbody>
</table>

Figure 2. Example ACGCA model predictions for *A. rubrum* based on a forest gap cycle with a 4-year open gap, a 15-year canopy closure period, and a 20-year closed forest canopy. Relative values of tree height (*H*), leaf biomass (*B_L*), and sapwood labile carbon (*C_S*) are shown. Six growth phases are predicted: (A) the tree is in a healthy state, growing according to the target allometry, (B) after experiencing several years of moderately low light (canopy closure period), the tree is in a static state, replacing senesced tissues according to the target allometry, (C) during the closed canopy period (low light), the tree depletes its sapwood labile carbon pool and transitions to a shrinking state, dropping tissues according to the reduced allometry, (D) upon experiencing a second gap (high light), the tree is in a recovering state because it has excess labile carbon to replace tissues lost during the shrinking phase, (E) the tree has recovered because it has rebuilt tissues to satisfy the target allometry and (F) the tree returns to the healthy state during a period of relatively high light (second open gap phase).
and thus are solved for in the model (e.g., radial growth, sapwood death, allocation and retranslocation). Hence, the only truly ‘free’ quantities are (i) the structural relationships, but these are well-informed by empirical studies and (ii) the physiological processes, but these are not the focus of this paper and thus have been reduced to a few simple empirical relationships.

**Carbon dynamics overview**

The first two modules give the temporal dynamics of the state variables. We consider six structural carbon (or biomass) compartments that can be distinguished by their functional roles: trunk sapwood, trunk heartwood, branch and coarse root (hereafter, ‘other’) sapwood, other heartwood, leaves and fine roots. Labile carbon includes potentially mobile carbon compounds (e.g., sugars and starch), and we consider two storage pools and one transient pool. The storage pools include labile carbon in sapwood, leaves and fine roots. The labile carbon in the sapwood differs from the leaf and fine root pool because the sapwood pool can be uncoupled from the structural compartments, and labile carbon can be retranslocated without destroying sapwood function. Conversely, the leaf and fine root labile pool is tightly coupled to the structural compartments and can only be retranslocated during the loss of leaf and fine root tissues. The transient pool contains recent photosynthesis and retranslocated labile carbon; this carbon is not associated with any particular organ, and it is immediately redistributed within the plant. The following two sections give the equations associated with the structural and labile carbon dynamics of a healthy tree.

**Structural carbon dynamics**

In a healthy tree, photosynthetic inputs exceed maintenance respiration demands, resulting in excess labile carbon that is temporally stored in the transient pool. This excess carbon is allocated to production processes associated with building new tissues: some amount of carbon is incorporated

Table 2. Parameters in the ACGCA model; values are derived from the literature for *P. taeda* (loblolly pine) and *A. rubrum* (red maple) (see Online Supplementary Data for further details).

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Unit</th>
<th>Parameter value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$x$</td>
<td>Crown curvature parameter</td>
<td>–</td>
<td>0.308</td>
</tr>
<tr>
<td>$\varepsilon$</td>
<td>Radiation-use efficiency</td>
<td>g gluc MJ$^{-1}$</td>
<td>4.5 6.75</td>
</tr>
<tr>
<td>$P_{max}$</td>
<td>Maximum photosynthetic rate</td>
<td>g gluc m$^{-2}$ year$^{-1}$</td>
<td>2100 2100</td>
</tr>
<tr>
<td>$C_{GL}$</td>
<td>Construction costs of producing leaves</td>
<td>g gluc g dw$^{-1}$</td>
<td>1.51 1.45</td>
</tr>
<tr>
<td>$C_{GR}$</td>
<td>Construction costs of producing fine roots</td>
<td>g gluc g dw$^{-1}$</td>
<td>1.30 1.25</td>
</tr>
<tr>
<td>$C_{SW}$</td>
<td>Construction costs of producing sapwood</td>
<td>g gluc g dw$^{-1}$</td>
<td>1.47 1.37</td>
</tr>
<tr>
<td>$R_{mL}$</td>
<td>Maintenance respiration rate of leaves</td>
<td>g gluc g dw$^{-1}$ year$^{-1}$</td>
<td>0.95 1.25</td>
</tr>
<tr>
<td>$R_{mR}$</td>
<td>Maintenance respiration rate of fine roots</td>
<td>g gluc g dw$^{-1}$ year$^{-1}$</td>
<td>0.75 0.75</td>
</tr>
<tr>
<td>$R_{mS}$</td>
<td>Maintenance respiration rate of sapwood</td>
<td>g gluc g dw$^{-1}$ year$^{-1}$</td>
<td>0.025 0.025</td>
</tr>
<tr>
<td>$S_{L}$</td>
<td>Senescence rate of leaves</td>
<td>year$^{-1}$</td>
<td>0.33</td>
</tr>
<tr>
<td>$S_{O}$</td>
<td>Senescence rate of coarse roots and branches</td>
<td>year$^{-1}$</td>
<td>0.05</td>
</tr>
<tr>
<td>$S_{R}$</td>
<td>Senescence rate of fine roots</td>
<td>year$^{-1}$</td>
<td>0.5</td>
</tr>
<tr>
<td>$\delta_{L}$</td>
<td>Labile carbon storage capacity of leaves</td>
<td>g gluc g dw$^{-1}$</td>
<td>0.11</td>
</tr>
<tr>
<td>$\delta_{R}$</td>
<td>Labile carbon storage capacity of fine roots</td>
<td>g gluc g dw$^{-1}$</td>
<td>0.08</td>
</tr>
<tr>
<td>$\gamma_{c}$</td>
<td>Maximum storage capacity of living sapwood cells</td>
<td>g gluc m$^{-3}$</td>
<td>265,000 131,000</td>
</tr>
<tr>
<td>$\gamma_{w}$</td>
<td>(Inverse) density of sapwood structural tissue</td>
<td>m$^3$ g dw$^{-1}$</td>
<td>6.67 x 10$^{-7}$ 6.67 x 10$^{-7}$</td>
</tr>
<tr>
<td>$\gamma_{x}$</td>
<td>Xylem conducting area to sapwood area ratio</td>
<td>–</td>
<td>0.62</td>
</tr>
<tr>
<td>$k$</td>
<td>Light extinction coefficient</td>
<td>–</td>
<td>0.55</td>
</tr>
<tr>
<td>$m$</td>
<td>Maximum relative crown depth</td>
<td>–</td>
<td>0.95 0.95</td>
</tr>
<tr>
<td>$\rho_{A}$</td>
<td>Wood density at zero radial growth</td>
<td>g dw m$^{-3}$</td>
<td>380,000 525,000</td>
</tr>
<tr>
<td>$\rho_{B}$</td>
<td>Wood density at maximum radial growth</td>
<td>g dw m$^{-3}$</td>
<td>380,000 525,000</td>
</tr>
<tr>
<td>$\rho_{R}$</td>
<td>Tissue density of fine roots</td>
<td>g dw m$^{-3}$</td>
<td>200,000 160,000</td>
</tr>
<tr>
<td>$r_{R}$</td>
<td>Average fine root radius</td>
<td>m</td>
<td>0.00027 0.00015</td>
</tr>
<tr>
<td>SLA</td>
<td>Specific leaf area</td>
<td>m$^2$ g dw$^{-1}$</td>
<td>0.0060 0.0141</td>
</tr>
<tr>
<td>$\eta$</td>
<td>Relative height at which trunk transitions from a paraboloid to a cone</td>
<td>–</td>
<td>0.71 0.64</td>
</tr>
<tr>
<td>$\eta_{B}$</td>
<td>Relative height at which trunk transitions from a neiloid to a paraboloid</td>
<td>–</td>
<td>0.045 0.045</td>
</tr>
<tr>
<td>$\phi_{H}$</td>
<td>Slope at H versus r curve at r = 0 m</td>
<td>–</td>
<td>220 263</td>
</tr>
<tr>
<td>$\lambda$</td>
<td>Proportionality between $B_{T}$ and $B_{O}$</td>
<td>–</td>
<td>0.95 0.95</td>
</tr>
<tr>
<td>$H_{max}$</td>
<td>Maximum tree height</td>
<td>m</td>
<td>42 27.5</td>
</tr>
<tr>
<td>SW$_{max}$</td>
<td>Maximum sapwood width</td>
<td>m</td>
<td>0.06 0.10</td>
</tr>
<tr>
<td>$f_{1}$</td>
<td>Fine root area to leaf area ratio</td>
<td>–</td>
<td>4.0 4.0</td>
</tr>
<tr>
<td>$f_{2}$</td>
<td>Leaf area to xylem conducting area ratio</td>
<td>–</td>
<td>2100 7000</td>
</tr>
</tbody>
</table>
Table 3. Important auxiliary variables in the ACGCA model.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\delta_W$</td>
<td>Labile carbon storage capacity of new sapwood</td>
<td>g gluc g dw$^{-1}$</td>
</tr>
<tr>
<td>$\delta_S$</td>
<td>Labile carbon storage capacity of bulk sapwood</td>
<td>g gluc g dw$^{-1}$</td>
</tr>
<tr>
<td>$v_O$</td>
<td>Sapwood-to-heartwood conversion rate of coarse roots and branches</td>
<td>year$^{-1}$</td>
</tr>
<tr>
<td>$v_T$</td>
<td>Sapwood-to-heartwood conversion rate of trunk</td>
<td>year$^{-1}$</td>
</tr>
<tr>
<td>$\rho_W$</td>
<td>Wood density</td>
<td>g dw m$^{-3}$</td>
</tr>
<tr>
<td>$B_S$</td>
<td>Biomass of ‘living’ sapwood</td>
<td>g dw</td>
</tr>
<tr>
<td>$C_S$</td>
<td>Maximum amount of labile carbon stored in sapwood</td>
<td>g gluc</td>
</tr>
<tr>
<td>$E$</td>
<td>Flux of excess labile carbon</td>
<td>g gluc year$^{-1}$</td>
</tr>
<tr>
<td>$f_L$</td>
<td>Fraction of excess labile carbon ($E$) allocated to leaves</td>
<td>–</td>
</tr>
<tr>
<td>$f_O$</td>
<td>Fraction of $E$ allocated to coarse roots and branches</td>
<td>–</td>
</tr>
<tr>
<td>$f_R$</td>
<td>Fraction of $E$ allocated to fine roots</td>
<td>–</td>
</tr>
<tr>
<td>$f_T$</td>
<td>Fraction of $E$ allocated to trunk</td>
<td>–</td>
</tr>
<tr>
<td>$H$</td>
<td>Tree height</td>
<td>m</td>
</tr>
<tr>
<td>$H_{TH}$</td>
<td>Height of trunk heartwood</td>
<td>m</td>
</tr>
<tr>
<td>$h_B$</td>
<td>Height at which trunk transitions from a neiloid to a paraboloid</td>
<td>m</td>
</tr>
<tr>
<td>$h_C$</td>
<td>Height at which trunk transitions from a paraboloid to a cone</td>
<td>m</td>
</tr>
<tr>
<td>$LA$</td>
<td>Total one-sided leaf area</td>
<td>m$^2$</td>
</tr>
<tr>
<td>$LAI$</td>
<td>Leaf area index</td>
<td>m$^2$/m$^2$</td>
</tr>
<tr>
<td>$r_B$</td>
<td>Trunk radius at neiloid–paraboloid transition</td>
<td>m</td>
</tr>
<tr>
<td>$r_C$</td>
<td>Trunk radius at paraboloid–cone transition</td>
<td>m</td>
</tr>
<tr>
<td>$R_C$</td>
<td>Crown radius</td>
<td>m</td>
</tr>
<tr>
<td>$R_{C,base}$</td>
<td>Crown radius at base of crown</td>
<td>m</td>
</tr>
<tr>
<td>$R_{C,max}$</td>
<td>Maximum potential crown radius at distance $mH$ from top of tree</td>
<td>m</td>
</tr>
<tr>
<td>$R_M$</td>
<td>Whole-plant maintenance respiration rate</td>
<td>g gluc year$^{-1}$</td>
</tr>
<tr>
<td>$SA$</td>
<td>Sapwood area at base of trunk</td>
<td>m$^2$</td>
</tr>
<tr>
<td>$SW$</td>
<td>Sapwood width (depth) at base of trunk</td>
<td>m</td>
</tr>
<tr>
<td>$V_C$</td>
<td>Volume of crown</td>
<td>m$^3$</td>
</tr>
<tr>
<td>$V_{C,base}$</td>
<td>Total crown volume from top of crown to base of crown</td>
<td>m$^3$</td>
</tr>
<tr>
<td>$V_T$</td>
<td>Volume of trunk</td>
<td>m$^3$</td>
</tr>
<tr>
<td>$V_{TH}$</td>
<td>Volume of trunk heartwood</td>
<td>m$^3$</td>
</tr>
<tr>
<td>$V_{TS}$</td>
<td>Volume of trunk sapwood</td>
<td>m$^3$</td>
</tr>
</tbody>
</table>

into new biomass, some is lost as growth respiration, and some is partitioned to storage within the newly produced tissues (e.g., Reynolds et al. 1980). At the same time, ‘old’ leaf, fine root, coarse root and branch tissues are lost due to senescence (or pruning) and a portion of sapwood is converted to heartwood.

A set of difference equations describe the structural carbon dynamics of a healthy tree. Let $B_i$ represent the structural biomass of tissue $i$, where $i = L$ (leaves), $R$ (fine roots), $TS$ (trunk sapwood), $TH$ (trunk heartwood), $T$ (bulk trunk), $OS$ (other sapwood), $OH$ (other heartwood) and $O$ (bulk other wood); recall that ‘other’ refers to branches and coarse roots. Let $E$ denote the flux of excess labile carbon available for growth ($E > 0$ for a healthy tree) and $f_i$ denote the fraction allocated to tissue $i$ ($i = L$, $R$, $T$ [or TS] and $O$ [or OS]). Let $C_{gL}$ be the construction cost and $\delta_L$ be the labile carbon storage capacity of tissue $i$ ($i = L$, $R$ and $W$ for newly produced sapwood). Let $\delta_S$ denote the actual concentration of labile carbon stored in bulk (‘old’) sapwood; $\delta_S$ and $\delta_W$ often differ because (i) the storage capacity of new sapwood may diverge from old sapwood due to, for example, variations in wood density and (ii) $\delta_S$ is reduced when labile carbon is retranslocated from old sapwood during static or shrinking periods. Finally, let $S_i$ be the senescence rate of tissue $i$ and $v_i$ be the sapwood-to-heartwood conversion rate of the trunk ($i = T$) and other woody tissues ($i = O$). The structural carbon dynamics are given by the following equations that simply define mass–balance relationships:

\[
\Delta B_L = \left( f_L(t) \cdot \frac{E(t)}{C_{gL} + \delta_L} - S_L \cdot B_L(t - \Delta t) \right) \cdot \Delta t,
\] (1A)

\[
\Delta B_R = \left( f_R(t) \cdot \frac{E(t)}{C_{gR} + \delta_R} - S_R \cdot B_R(t - \Delta t) \right) \cdot \Delta t,
\] (1B)

\[
\Delta B_{TS} = \left( f_T(t) \cdot \frac{E(t)}{C_{gTS} + \delta_W(t)} - v_T(t) \cdot B_{TS}(t - \Delta t) \right) \cdot \Delta t,
\] (1C)

\[
\Delta B_{TH} = \left[ 1 + \delta_S(t) \right] \cdot v_T(t) \cdot B_{TH}(t - \Delta t) \cdot \Delta t,
\] (1D)

\[
\Delta B_{OS} = \left( f_O(t) \cdot \frac{E(t)}{C_{gOS} + \delta_W(t)} - (S_O + v_O(t)) \cdot B_{OS}(t - \Delta t) \right) \cdot \Delta t,
\] (1E)

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\begin{equation}
\Delta B_{OH} = (1 + \delta_s(t)) \cdot v_0(t) \cdot B_{OS}(t - \Delta t) - S_O \cdot B_{OH}(t - \Delta t) \cdot \Delta t. \tag{1F}
\end{equation}

Total trunk and other woody biomass are \( B_T = B_{TH} + B_{OH} \) and \( B_O = B_{OS} + B_{OH} \), respectively.

Equations (1A) and (1B) describe changes in leaf and fine root biomass, and the first term on the right-hand side (RHS) is the ‘production’ term. The quantity \( 1/(C_{gi} + \delta) \) gives the number of grams of biomass of tissue \( i \) that can be constructed from 1 g of glucose; when multiplied by the grams of glucose invested into the tissue per year, \( f_i \cdot E \), this gives the amount of new tissue constructed per year. For every gram of tissue produced, \( C_{gi} \) grams of glucose are lost to growth respiration and \( \delta_i \) grams are allocated to storage in the new tissue. The second term on the RHS involving \( S_i \) is the ‘loss’ term. Equations (1C) and (1E) describe changes in trunk and other sapwood biomass, respectively. The dead and static states are modified from Eq. (3) (see Online Supplementary Data).

### Labile carbon dynamics

The dynamics of the labile pools are coupled to the structural pools to varying degrees depending on the physiological state of the tree. The labile carbon dynamics described below are unique to a healthy tree. These pools are modeled similar to the pool balance-organ demand scheme described by Reynolds et al. (1980), but our approach differs because we consider a sapwood pool and use allometrically constrained rules for allocating labile carbon to storage and growth.

#### Stored labile carbon

Let \( C_S \) denote the amount of labile carbon stored in all sapwood; the dynamics of \( C_S \) are given by

\begin{equation}
\Delta C_S = \left\{ \begin{array}{c}
E(t) \cdot \frac{\delta_w(t)}{C_{gw} + \delta_w(t)} \cdot (f_L(t) + f_o(t)) - \left( \delta_S(t) \cdot [v_0(t) + S_O] \cdot B_{OS}(t - \Delta t) + v_T(t) \cdot B_{TS}(t - \Delta t) \right) \end{array} \right\} \cdot \Delta t. \tag{3}
\end{equation}

The first term on the RHS is the amount of carbon that is partitioned to storage to balance the production of new sapwood. The second term describes the losses of stored carbon due to (i) retranslocation to the transient pool during senescence of branches and coarse roots and (ii) incorporation into newly formed heartwood. Expressions of \( \Delta C_S \) for the other physiological states are modified from Eq. (3) (see Online Supplementary Data).

For modeling convenience, we assume that retranslocation of labile carbon from leaf and fine root tissue is 100% efficient. Labile carbon in senescing leaves and fine roots is retranslocated to the transient pool and is subsequently used for maintenance and growth processes. Thus, \( C_{LR} \) is

\begin{equation}
C_{LR}(t) = \delta_L \cdot B_L(t) + \delta_R \cdot B_R(t). \tag{4}
\end{equation}

Retranslocation of labile carbon is less efficient (Chapin et al. 1990), but the lack of sufficient data on recycling makes it difficult to quantify retranslocation efficiency. Additionally, laboratory methods for measuring construction costs are based on tissues that contain structural (e.g., cellulose) and nonstructural (e.g., carbohydrates) compounds (see Chiariello et al. 1989, Griffin 1994). Thus, the structural carbon compartments in the ACGCA model can be thought of as containing truly structural compounds and some nonstructural materials that do not have the potential to be retranslocated.

The ability of sapwood to store labile carbon is partly determined by its anatomy (e.g., Hoch et al. 2003). Sapwood is composed of xylem elements and living cells, and the sapwood volume of the trunk can be written as \( V_{TS} = V_X + V_W + V_C \), where \( V_X \), \( V_W \) and \( V_C \) are the total volumes of xylem conduit lumens, cell walls (and other structural components) and living cell lumens, respectively. Three key assumptions are (i) \( V_W \) is proportional to trunk sapwood mass: \( V_W = \gamma_W \cdot B_{TS} \), (ii) the total cross-sectional area of the conduit lumens is proportional to the cross-sectional area of sapwood (see Eq. (14)): \( V_X = \gamma_X \cdot V_{TS} \) and (iii) the maximum potential amount of labile carbon
stored in the trunk sapwood \( C_{TS}^* \) is proportional to \( V_C : C_{TS}^* = \gamma_C \cdot V_C \). Based on these assumptions, the maximum potential amount of labile carbon stored in the sapwood of all woody tissues is

\[
C_s(t) = \gamma_C \cdot \left( (1 - \gamma_X) \cdot \frac{V_{TS}(t)}{B_{TS}(t)} - \gamma_w \right) \cdot B_s(t),
\]

where \( B_s = B_{TS} + B_{OS} \). The maximum labile carbon storage capacity of new sapwood (\( \delta_w \)) is

\[
\delta_w(t) = \frac{\gamma_C \cdot (1 - \gamma_X - \gamma_w \cdot \rho_w(t))}{\rho_w(t)}.
\]

Equation (6) is derived from (5) by assuming \( \Delta V_{TS} = \rho_w(t) \cdot \Delta B_{TS} \) and \( \Delta V_S = \rho_w(t) \cdot \Delta B_S \), where \( V_S \) is the volume of bulk sapwood and \( \rho_w \) is the wood density of new sapwood. The actual concentration of labile carbon stored in the bulk sapwood (\( \delta_s \)) is

\[
\delta_s(t) = \frac{C_s(t - \Delta t)}{B_s(t - \Delta t)}.
\]

**Transient labile carbon.** The flux of excess labile carbon (\( E \)) defines the size of the transient pool (given by \( E \cdot \Delta t \)), where \( E \) is defined as

\[
E(t) = P_G(t) \cdot LA(t - \Delta t) - R_M(t) + \delta_s(t) \cdot S_0 \cdot B_{OS}(t - \Delta t) + \sum_{i=L,R} \delta_i \cdot S_i \cdot B_i(t - \Delta t).
\]

\( P_G \) is annual gross photosynthetic rate, \( LA \) is total one-sided leaf area, \( R_M \) is whole-plant maintenance respiration and the last two terms are inputs from labile carbon retranslocation that occurs during senescence. \( E > 0 \) for healthy, recovering and recovered trees, but \( E \) may be negative for trees in the static or shrinking state. Equations (4–8) hold for all physiological states.

**Alloometric relationships.**

We assume that the trunk and crown allometries are independent of the physiological state. A subset of allometric relationships, however, depend on the physiological state such that a tree grows (or shrinks) according to a target (for a healthy tree) or reduced (for an unhealthy tree) allometry, and we describe both allometries in this section. The target allometry relates all structural compartments to trunk radius, but the nontrunk structural compartments are decoupled from trunk radius under the reduced allometry. Although many quantities in the following equations depend on time (\( t \) or \( t - \Delta t \)), for convenience, we generally drop the reference to time in this section.

**Trunk allometries.** We assume that the trunk taper can be described by three sections: the base is modeled as a neiloid, the middle as a paraboloid and the top as a cone (Recknagel and Bentley 1919, Osawa 1992, Valentine and Gregoire 2001). Let \( r \) be the radius at the base of the trunk, \( r_b \) and \( h_b \) be the radius and height, respectively, at which the trunk transitions from a neiloid to a paraboloid, \( r_c \) and \( h_c \) be the radius and the height of transition from a paraboloid to a cone, and \( H \) be the tree height (\( h_b < h_c < H \)). The volume of the trunk is the sum of the volumes of the three sections:

\[
V_T = \frac{\pi \cdot r^2}{4 \cdot H^2} \left\{ H^2 - (H - h_b)^2 \right\} + \frac{\pi \cdot r_b^2}{2 \cdot (H - h_b)} \left\{ h_b^2 - h_c^2 + 2 \cdot H \cdot (h_c - h_b) \right\} + \frac{\pi \cdot r_c^2}{3} \cdot (H - h_c).
\]

We let \( h_b = \eta_b \cdot H \) and \( h_c = \eta \cdot H \) (e.g., Valentine and Gregoire 2001), and we model \( H \) as an asymptotic function of \( r \) (e.g., Pacala et al. 1996):

\[
H = H_{\text{max}} \cdot \left\{ 1 - \exp \left( -\frac{\phi_H}{H_{\text{max}}} \cdot r \right) \right\},
\]

where \( H_{\text{max}} \) is the maximum tree height and \( \phi_H \) is the slope of the \( H \) versus \( r \) curve at \( r = 0 \) (\( \phi_H > 0 \)).

We assume that sapwood width along the length of the trunk is constant and equal to sapwood width at the base, \( SW \), and that sapwood width converges to the trunk radius near the top. Thus, the radius of the heartwood at the base is \( r_b = SW \), and \( r_b \) by \( r_b - SW \). We let \( r_c = SW \) and \( H \) by the height of the heartwood section, \( H_{TH} \):

\[
H_{TH} = \frac{1}{r_c} \left\{ H \cdot (r_c - SW) + h_c \cdot SW \right\}.
\]

Alternate formulations for \( V_{TH} \) are used if the heartwood terminates inside the paraboloid or neiloid sections (see Online Supplementary Data). The trunk sapwood volume is \( V_{TS} = V_T - V_{TH} \).

We assume that the entire trunk is sapwood for small trees. As the tree grows, \( SW \) eventually reaches a maximum and constant value, paralleled by the onset of heartwood formation. Given \( SW \), the cross-sectional area of the sapwood (\( SA \)) at the base is given by simple geometry such that

\[
SA = \pi \cdot SW \cdot (2 \cdot r - SW).
\]

We also assume that the total cross-sectional area of xylem conduit lumens (\( XA \)) at the base of the tree is proportional to sapwood area:

\[
XA = \gamma_X \cdot SA.
\]
Crown allometries  This module describes a tree’s crown radius ($R_C$) at distance $z$ from the top of its crown. $R_C$ is given by the crown shape model of Purves et al. (2007)

$$R_C(z) = R_{C,max} \cdot \left( \frac{\min[z, m \cdot H]}{m \cdot H} \right)^z,$$  

(15)

where $R_{C,max}$ is the maximum potential radius at a crown ratio (potential crown depth/$H$) of $m$ and $z$ describes the curvature of the crown. The actual crown ratio is given by $(1 - \eta)$. If $m > (1 - \eta)$, then the radius at the base of the crown is given by $R_{C,base} = R_C(z = (1 - \eta) \cdot H) = R_{C,max} \cdot (1 - \eta) / m$. We describe $R_{C,max}$ as a function of $r$ based on Purves et al. (2007) (see Online Supplementary Data). Based on Eq. (15), the volume of the tree’s crown from the top to distance $z$ from the top is

$$V_C(z) = \pi \cdot R_{C,max}^2 \cdot \frac{z}{1 + 2 \cdot z \cdot \left( \frac{z}{H + m} \right)^z},$$

(16)

for $z \leq (1 - \eta) \cdot H$. The volume of the crown between the top and the base of the crown is given by $V_{C,base} = V_C(z = (1 - \eta) \cdot H)$. $V_C$ is used to compute the tree’s leaf area index (LAI). We assume that leaf production is ‘volume filling’ (e.g., West et al. 1999) such that the tree’s leaf area is evenly distributed within the volume of the crown. Thus, the tree’s LAI between the top and the distance $z$ is

$$\text{LAI}(z) = \frac{LA}{\pi \cdot R_{C,base}^2 \cdot \left( \frac{V_C(z)}{V_{C,base}} \right)}.$$

(17)

Target allometry  The above trunk and crown allometries apply to both the target and the reduced allometries, but relationships between other components differ between the allometries. In the target allometry, we assume proportionality between leaf area, fine root area and xylem lumen area that implicitly reflect water transport constraints similar to the ‘pipe model’ (Shinozaki et al. 1964):

$$RA = f_1 \cdot LA,$$  

(18A)

$$LA = f_2 \cdot XA,$$  

(18B)

where $RA$ is the total surface area of the fine roots and $f_1$ and $f_2$ are the constants of proportionality.

We allow wood density to depend on radial growth rate ($\Delta r / \Delta t$), and we assume (i) upper and lower limits to $\rho_w$, (ii) $\Delta r$ should not exceed $SW_{max}$ and (iii) $\rho_w$ is a linear function of $\Delta r / \Delta t$:

$$\rho_w(t) = \begin{cases} \rho_A - \frac{\rho_{A - \rho_B}}{SW_{max}} \cdot \Delta r < SW_{max} \\ \rho_B \Delta r \geq SW_{max} \end{cases}$$

(19)

Equation (19) is flexible because it allows for positive (Bergés et al. 2000, Bouriaud et al. 2005), negative (Mäkinen et al. 2002, DeBell et al. 2004, Muller-Landau 2004, King et al. 2005) and uncorrelated (DeBell et al. 2004, Bouriaud et al. 2005) relationships between $\rho_w$ and radial growth.

Finally, we assume that sapwood and heartwood biomass of coarse roots and branches are proportional to sapwood and heartwood biomass of the trunk such that

$$B_{OS} = \lambda_S \cdot B_{TS},$$

(20A)

$$B_{OH} = \lambda_H \cdot B_{TH},$$

(20B)

where $\lambda_S$ and $\lambda_H$ are constants of proportionality.

Reduced allometry  During nonhealthy states, all trunk structural variables ($B_T$, $B_{TS}$, $B_{TH}$, $r$, $H$, $SA$, etc.) are constant, and Eqs. (18B–20B) change because excess loss of leaf, fine root and other woody tissue breaks the relationships between these compartments and trunk radius. For example, LA is no longer directly proportional to $XA$ because $LA$ can change but $XA$ cannot change. Under the reduced allometry, all nontrunk compartments are expressed as functions of LA (versus $r$ as in the target allometry). The fine root allometry is still as defined in Eq. (18A), but the allometries for the other woody tissues are given by

$$B_{OS} = LA \cdot \frac{\lambda_S}{\lambda_S} \cdot \frac{B_{TS}}{BS},$$

(21A)

$$B_{OH} = B_{OS} \cdot \frac{\lambda_H}{\lambda_S} \cdot \frac{B_{TH}}{BS},$$

(21B)

Thus, the allometries of nontrunk compartments are determined by the current state of the trunk (i.e., $SA$, $B_{TS}$ and $B_{TH}$). Equations (21A) and (21B) replace (20A) and (20B) upon switching between the target and reduced allometries, producing a smooth transition between the allometries.

Finally, we assume that the wood density of coarse root and branch sapwood produced during reduced allometry phases is equal to the wood density of the bulk trunk sapwood such that

$$\rho_w = \frac{B_{TS}}{V_{TS}}.$$  

(22)

Within a given reduced allometry phase, $B_{TS}$, $V_{TS}$ and $\rho_w$ are constant, and Eq. (22) replaces (19).

Physiology  The physiology module includes descriptions of photosynthesis and maintenance respiration. For ease of development and initial application, we chose to implement a very simple, empirical physiology module, especially with respect to photosynthesis. A future goal is to incorporate a more mechanistic, faster time-step representation of carbon fluxes. The current version uses a radiation-use type model (e.g., Landsberg and Waring 1997, Medlyn et al. 2003) for annual gross carbon gain ($P_G$), which represents the total amount of labile carbon produced during photosynthesis:

$$P_G(t) = \varepsilon \cdot \text{APAR}(t).$$

(23)
where $\varepsilon$ is radiation-use efficiency and APAR is absorbed photosynthetically active radiation (PAR), both of which are defined on an annual time scale. The APAR partly depends on the LAI of the tree crown and the surrounding forest canopy; see the detailed description in the section Simulation experiments.

Total annual maintenance respiration is determined by the mass-specific respiration rates and total mass of living leaf (L), fine root (R) and sapwood (S) tissue:

$$ R_M(t) = R_{ml} \cdot B_L(t - \Delta t) + R_{mr} \cdot B_R(t - \Delta t) + R_{ms} \cdot B_S(t - \Delta t), $$

(24)

where $R_{mi}$ is the mass-specific respiration rate of tissue $i$. We assume that the effective amount of respiring sapwood, $B_S$, is composed of a baseline maintenance component and a living tissue component whose energy requirements depend on the carbon storage status of the cells

$$ B_S(t) = \left(1 - \frac{\gamma_W}{1 - \gamma_S} \cdot \frac{B_{TS}(t)}{V_{TS}(t)} \right) \cdot \left[ B_S(t) + \frac{C_S(t)}{C_1} \cdot B_{TS}(t) \right]. $$

(25)

The fraction of sapwood that is composed of living cells and cell walls is described by \(1 - \frac{\gamma_W}{1 - \gamma_S} \cdot \frac{B_{TS}(t)}{V_{TS}(t)}\); when multiplied by $B_S$, this gives the total mass of structural and living tissue in the sapwood (i.e., baseline tissue). Multiplication by the second term gives the total mass associated with stored labile carbon. Thus, storage increases respiration demands (e.g., Lambers et al. 1998, p 315), and a reduction in the amount of respiring sapwood due to drawdown of labile carbon is consistent with loss of activity or death of living cells during retranslocation (e.g., Spicer 2005).

Allocation and retranslocation

Fundamental to the ACGCA model is its ability to capture dynamic allocation and retranslocation by explicitly solving for these processes such that allocation and growth satisfy the structural allometries. This is in contrast to many existing tree growth models that specify fixed equations for the fractional allocation terms (i.e., the $f_i$’s) (see review by Le Roux et al. 2001), posing a potential problem because it is nearly impossible to measure allocation of labile carbon in plants in the field (e.g., Cannell and Dewar 1994), thus making it difficult to parameterize such models. Additionally, many allocation schemes are derived from empirical relationships (e.g., Sharpe and Rykiel 1991, Friedlingstein et al. 1999) and do not share the same level of physiological detail in companion photosynthesis and respiration models (Cannell and Dewar 1994). Considerations of source-sink demands and the biophysics of transport resistance have yielded theoretical models of allocation (Thornley 1972a, 1972b, Cannell and Dewar 1994), but they do not assure that the modeled plant will allocate carbon in such a way that growth is consistent with allometric constraints. More recently, a set of approaches have emerged for coupling allometries and physiology-based structural carbon dynamics to model ‘allocation’ (e.g., West 1993, Mäkelä 1999, King 2005). Although a step in the right direction, these approaches do not consider labile carbon; instead, they solve for the distribution of structural biomass, which is different from the allocation of labile carbon (Dickson and Isebrands 1993).

The ACGCA model bypasses the aforementioned problems such that allocation is solved for directly and the solutions depend on the physiological state of the tree, and we outline the approach as applied to a healthy tree. First, matching the allometries and the structural carbon dynamics means that the following must be true:

$$ \Delta B_{OS} = \dot{i}_S \cdot \Delta B_{TS}, $$

(26A)

$$ \Delta B_{OH} = \dot{i}_H \cdot \Delta B_{TH}, $$

(26B)

$$ \frac{\Delta LA}{SLA} = \Delta B_L, $$

(26C)

$$ \rho_R \cdot \frac{R_B}{2} \cdot \Delta V_T = \Delta B_T, $$

(26D)

The $\Delta B_i$’s represent the carbon dynamics (Eq. (1A–1F)), and the allometries are incorporated through $\Delta LA$, $\Delta RA$, $\rho_W$, and $\Delta V_T$, which are functions of $r$ through the target allometry (Eqs. (9–20)). SLA is specific leaf area and $\rho_R$ and $r_R$ are the tissue density and average radius of fine roots.

After substituting the carbon dynamics and allometric equations into Eqs. (26A–26E), the resulting equations are nonlinear functions of $\Delta r$ that must be solved numerically. We employed a simple root-finding routine that balances ‘supply’ (i.e., $E$, which is independent of $\Delta r$) and ‘demand’ (labile carbon cost associated with producing new biomass, which depends on $\Delta r$) to solve for $f_L$, $f_R$, $f_T$, $f_O$, $v_O$ and $\Delta r$ (see the Online Supplementary Data). The root-finding routine is required for the healthy and recovered states, but analytical solutions are available for the other physiological states (see Online Supplementary Data).

Application of the ACGCA model

We demonstrate the behavior of the ACGCA model by exploring its predicted growth and allocation patterns for two ecologically-distinct species. We focus on $P$. taeda (loblolly pine) and $A$. rubrum (red maple) because (i) they are widespread throughout temperate forests of the eastern USA (Baker and Langdon 1990, Walters and Yawney 1990, Little 2004), (ii) they are commonly studied, and thus
there is sufficient information for obtaining realistic parameter values and (iii) they exhibit contrasting ecological strategies. For example, *P. taeda* is a shade-intolerant, late-successional, commercially important species that primarily occurs in the Southeast (Baker and Langdon 1990); *A. rubrum* is a fairly shade-tolerant, mid/late-successional species whose range extends to more northerly latitudes (Walters and Yawney 1990). Despite these differences, the two species co-occur in mid-successional stands where their ranges overlap such as in the Southeast (Billings 1938, Oosting 1942, Burns and Honkala 1990, Carey 1992, Bragg 2004).

These species differ in several ecological traits that may contribute to their contrasting shade-tolerance strategies. *Pinus taeda* retains its needles for about 3 years (FNA 1993), while *A. rubrum* is a broad-leaved, winter-deciduous tree. The sapwood of *P. taeda* is almost entirely composed of tightly packed tracheids, whereas the diffuse-porous sapwood of *A. rubrum* contains a significant amount of living parenchyma and comparatively little conducting tissue (e.g., Haygreen and Bowyer 1982). Xylem anatomy helps to explain dissimilar water relations of *P. taeda* and *A. rubrum* (Maherali et al. 2006) and may also affect wood density and labile carbon storage. The large conduit lumen component in *P. taeda* likely results in lower wood density and a reduced ability to store labile carbon relative to *A. rubrum*. We use the ACGCA model to explore how differences in these traits may influence growth, allocation and mortality of *A. rubrum* and *P. taeda* under different light regimes.

**Simulation experiments**

We conducted a simulation experiment that varied the light levels, and the purpose of this experiment is twofold. First, we use the simulations to demonstrate a suite of behaviors that the ACGCA model is capable of capturing. Second, the simulations provide insight into the potential differential responses of *A. rubrum* and *P. taeda* to changes in light. Although intended for demonstration purposes, we defined the light environments to be representative of forest canopy gap dynamics.

The gap dynamics are defined by three phases that are sequentially repeated: gap formation (i.e., open gap), gap closure and closed canopy (Figure 3A). We considered three levels for the duration of the open gap phase (4, 6 and 8 years), five for the gap closure phase (5, 10, 15, 25 and 45 years), and five for the time between gaps (20, 35, 50, 100 and 200 years). These scenarios are comparable with other simulation studies (e.g., Valverde and Silverstowns 1997). The time between gaps is equivalent to gap-forming disturbance rates of 5, 3, 2, 1 and 0.5% per year, respectively, spanning the range of rates estimated for temperate forests (Runkle and Yetter 1987, Cipollini et al. 1994, Ziegler 2002). Consistent with the time frames considered here, canopy closure can occur within several years (e.g., 8–9 years, Cipollini et al. 1994) or may take as long as 15 (Kull et al. 1999) to 45 years (Runkle and Yetter 1987). The duration of the closed canopy phase, which ranged from 1 year to 191 years, is given by the time between gaps minus the time associated with gap formation and closure. Some combinations were inconsistent (e.g., 45 years of gap closure and 20 years between gaps) and a total of 62 combinations yielded consistent light regimes.

The gap dynamic scenarios are used to define temporal variability in the target tree’s light environment. In doing so, there are three scenarios that we must consider based on the height of the forest canopy (*H*<sub>F</sub>) relative to the height of the target tree (*H*): (i) the tree’s crown is completely

**Figure 3.** Schematic of a gap cycle, defined by three phases that are sequentially repeated: gap formation (open gap), gap closure and closed canopy. (A) Forest canopy leaf area index (LAI<sub>F</sub>) and canopy height (*H*<sub>F</sub>) depend on the gap cycle phase such that (i) LAI<sub>F</sub> = *H*<sub>F</sub> = 0 during an open gap, (ii) total LAI<sub>F</sub> and *H*<sub>F</sub> increase linearly to their respective maximums (LAI<sub>F,max</sub> and *H*<sub>F,max</sub>) during canopy closure and (iii) total LAI<sub>F</sub> = LAI<sub>F,max</sub> and *H*<sub>F</sub> = *H*<sub>F,max</sub> during closed canopy. (B) The relative LAI profile (LAI<sub>F</sub>(d)/LAI<sub>F</sub>) is a function of relative height (*d*/*H*<sub>F</sub>), where *d* is the distance from the ground. We choose values for LAI<sub>F</sub> and *H*<sub>F</sub>, as given in (A), based on studies conducted in forest types similar to those supporting *P. taeda* or *A. rubrum* (Runkle and Yetter 1987, Ellsworth and Reich 1993, Fahey et al. 1998, Le Dantec et al. 2000, Norby et al. 2003, McCarthy et al. 2006).
PARmax is the maximum PAR above the tree and forest canopy (Figure 3B) based on LAI profiles in Strachan and McCaughey (1996) and Fahey et al. (1998). See the Online Supplementary Data for further details.

We employ the Beer–Lambert equation (as described in Thornley 1996) to model APAR in Eq. (23) based on the target tree’s LAI and H and the forest canopy LAI F and H. If the tree satisfies the first scenario (H > H), then

\[
APAR(t) = \frac{PAR_{\text{max}} \cdot \{1 - \exp(-k \cdot \text{LAI}(t - \Delta t))\}}{\text{LAI}(t - \Delta t)}.
\]

PARmax is the maximum PAR above the tree and forest canopies, and k is the light extinction coefficient of the target tree’s canopy. Based on four years (2001–2004) of monthly PAR records for 24 weather stations in North Carolina (CRONOS 2004), we assumed that PARmax \(\lesssim 2060\ \text{MJ}\ \text{m}^{-2}\ \text{year}^{-1}\). If the tree is associated with the other scenarios (H < H), then it competes for light with the surrounding forest, and APAR is based on modifications of Eq. (27) (see the Online Supplementary Data). The details about the light environment presented here are not integral to the ACGCA model, but simply provide realistic input values for APAR.

The ACGCA model describes the behavior of an individual tree at an annual resolution. We obtained solutions to tree growth every 0.0625 years because numerical convergence is achieved for \(\Delta t \leq 1/16\) years. The initial states were: (i) \(r(t = 0) = 0.005\ \text{m}\), (ii) \(C_g(t = 0) = C_g^0(t = 0) = 0\) g glucose and (iii) initial size (biomass) of all state variables satisfy the target allometry. We ran the model for a maximum of 300 simulation years.

ACGCA model behavior

The ACGCA model produces a suite of predictions, but we choose to focus on a few key predictions. We refer to model results under the A. rubrum and P. taeda parameterizations as ‘A. rubrum’ and ‘P. taeda’, respectively, and we first discuss a subset of results that illustrate diverse model behavior in terms of each species’ predicted physiological states, growth, labile carbon and allocation patterns. We first examine four scenarios (see Figure 4) that resulted in one of the four possible outcomes: (i) A. rubrum survived the 300-year simulation period, but P. taeda died, (ii) P. taeda survived, but A. rubrum died, (iii) both A. rubrum and P. taeda survived and (iv) both A. rubrum and P. taeda died. Then, we highlight the results of the 62 different gap dynamics scenarios in terms of implications for A. rubrum and P. taeda growing under real field conditions.

Physiological states

Both species experienced all five states characteristic of living trees (i.e., healthy, static, shrinking, recovering and recovered; Figures 1 and 4), and both die as a result of severe low-light stress (Figure 4D). The most common transitions predicted by the model for living trees were healthy to static (i.e., transition 1, Figure 1), static to shrinking (transition 2a, Figure 1), shrinking to recovering (transition 3a, Figure 1), recovering to recovered (transition 4a, Figure 1), and recovered to healthy (transition 5a, Figure 1). In the examples considered here, if a tree survived an individual gap cycle, then it experienced all five of these transitions (Figure 4). For trees that died, death occurred during the first gap cycle due to prolonged low-light stress that resulted in the depletion of stored labile carbon (Figure 4A, B and D).

For trees that survived the 300-year period, they spent a large fraction of the time either in a healthy state or shrinking state, depending on the length of the closed canopy phase. In scenario (iii) – short time between gaps and relatively short closed canopy phase – A. rubrum and P. taeda survived the 300-year period, and each spent about 40% of the time in a healthy state, growing along their target allometries during the open gap and initial part of the canopy closure phases (Figure 4C). Each also spent about 37% of the time in a shrinking state, dropping tissues according to their reduced allometries, which generally occurred during the latter part of each closed canopy phase. Acer rubrum survived the entire length of scenario (i) (Figure 4A) and P. taeda survived scenario (ii) (Figure 4B). Both scenarios have relatively long closed canopy periods, and the trees spent most of the time in the shrinking state (57% for A. rubrum, 75% for P. taeda) and about 22–25% of the time in a healthy, growing state.

If we consider scenario (iii) where both species survived (Figure 4C), both transition back-and-forth between their target and reduced allometries depending on their labile carbon status. As the trees grow larger and support more leaf and fine root tissue relative to sapwood tissue, the length of time that they spend in the healthy state (target allometry) decreases. That is, as the trees grow in size, maintenance demands begin to exceed labile carbon storage capabilities. This may be particularly true for P. taeda, which has a significantly reduced capacity to store labile carbon in its sapwood compared to A. rubrum (Figure 4C, top panel). For example, during each of the six gap cycles as shown in Figure 4C, the maximum amount of labile carbon stored in P. taeda’s sapwood is about 1/10 of that stored by A. rubrum, yet P. taeda supports a lower but somewhat comparable amount of leaf tissue. Living tissues such as leaves have high maintenance demands, and P. taeda’s carbon stores were only able to meet these
Figure 4. Example ACGCA simulation results for four of the gap dynamics scenarios: (A) open gap phase = 6 years, gap closure period = 15 years and time between gaps = 50 years, (B) open gap = 4 years, closure = 45 years and time between gaps = 200 years, (C) open gap = 8 years, closure = 25 years, and time between gaps = 50 years and (D) open gap = 6 years, closure = 25, and time between gaps = 200 years. The bars above each panel indicate the gap cycle phase: open bars = open gap, gray bars = canopy closure and black bars = closed canopy. Predicted temporal dynamics for sapwood labile carbon ($C_S$), total leaf mass ($B_L$) and tree height ($H$) are shown for $A.\ rubrum$ (filled circles) and $P.\ taeda$ (open circles), where the symbols indicate transitions between physiological states (Figure 1).
demands in 12 of the 62 gap scenarios (i.e., survived the 300-year period), whereas *A. rubrum* was able to meet these demands in 34 of the 62 scenarios.

**Growth patterns and allometric relationships**

A simple, two-phase power function emerges from the ACGCA model that relates the biomass of fine roots and leaves to the biomass of the trunk under the target allometry such that $B_L + B_R = a \cdot (B_T)^b$. The values of the coefficients $a$ and $b$ depend on the age/size of the tree and the parameter values used in the model, and thus the coefficients differ between *A. rubrum* and *P. taeda* (especially $a$, and to a lesser extent, $b$). The power function is consistent with a general theory of allometric scaling and associated data on biomass partitioning for a variety of tree species (Enquist and Niklas 2002, Niklas and Enquist 2002a, 2002b). Theory predicts a scaling exponent of 3/4, but the ACGCA model predicts exponents between 2/3 and 3/4 according to their associated power law functions for mature/large trees.

The ACGCA model suggests that unhealthy trees will diverge from the allometric scaling rule. Consider scenario (iii) shown in Figure 4C, during the first open gap and gap closure period, both species build biomass and progress ‘upward’ along the power laws for young/small trees (Figure 5); *P. taeda* and *A. rubrum* grow along this power law for the first eight and 15 years, respectively, before transitioning to the power law for mature/large trees.

In scenario (iii), the transition between the two power laws occurs before the first canopy closure phase. About 3 years after canopy closure, *P. taeda* diverges from its target allometry and begins shrinking along its reduced allometry, and *A. rubrum* also begins to shrink along its reduced allometry about 7 years following canopy closure. For both species, movement along the reduced allometry is depicted by vertical spurs of points shown in Figure 5. Upon exposure to high light during the second gap, *P. taeda* and *A. rubrum* grow in size along their reduced allometries (recovering state), retracing the paths created by their previous shrinking states, until they reach their respective target allometries (recovered). Once again, they begin building biomass according to their associated power law functions for mature/large trees.

**Labile carbon and dynamic allocation**

To illustrate the features of the predicted labile carbon dynamics, we focus on results obtained for *A. rubrum* based on scenario (i) (Figures 4A and 6). The transient labile carbon pool (i.e., $E \cdot \Delta t$) is very sensitive to changes in light. Upon exposure to high light during gap formation, $E$ immediately increases by a factor of 10 or more compared to the previous closed canopy (low light) phase (Figure 6A). Increases in $E$ enable the tree to escape the shrinking state experienced during the previous closed canopy phase, thereby allowing it to grow in size (see Figures 6A and 4C). Thus, additional tissues are no longer dropped, and retranslocation of labile carbon (Figure 6B) is solely due to normal senescence of nontrunk tissues. Retranslocation rates increase with time during the high-light periods as a direct product of the tree growing in size, whereby the absolute mass of tissues lost during senescence also increases. Growth during the recovering and healthy states (i.e., during gap formation) results in the production of sapwood and replenishing of the labile reserves (Figure 6C), but the short duration of the high-light episodes precludes the sapwood labile pool from recovering to its full potential (Figure 6D).

Upon canopy closure, $E$ rapidly drops due to reduced carbon gain associated with low light (Figure 6A), compounded by a reduction in photosynthetic leaf area that occurs during the shrinking state (see $B_{tr}$; Figure 4C). At some point during each closed canopy period, the tree must supplement $E$ with additional labile carbon to maintain its size. Rebuilding of senesced tissues during the static state is made possible by retranslocating labile carbon from the sapwood. The tree is initialized with a sapwood pool that is at its maximum capacity (Figure 6D, initial open gap), and retranslocation from this relatively large reserve keeps the tree from transitioning to a shrinking state during canopy closure and the initial closed canopy phase. When the tree enters a static state during closed canopy, there is a spike in the total retranslocation rate (see large values of $R_{tot}$, Figure 6B), which is attributed to the enhanced retranslocation from the sapwood that accounts for nearly 100% of the retranslocation during this phase (Figure 6F).
Retranslocation from the sapwood in the absence of trunk growth results in a drawdown of the sapwood reserves to levels that are many orders of magnitude less than the potential storage capacity (Figure 6C and D).

When the sapwood labile pool is nearly depleted, then the relative contribution of the sapwood to total retranslocation decreases back to 60–80% depending on the size of the tree (Figure 6F). At this point, additional branches, leaves and roots are dropped (e.g., Figure 4C), and the associated labile carbon is retranslocated to satisfy the maintenance demands of existing tissues and to grow a limited amount of structural tissue, thereby keeping the tree on the reduced allometry. At this point, the tree transitions from a static to shrinking state, and the relative contribution of the sapwood to total retranslocation remains high (see $f^*_L$ versus $f^*_S$ in Figure 6E versus F). However, total retranslocation is low (Figure 6B) given that the total labile pool is small during the shrinking state (Figure 6C). A small amount of branch and coarse root sapwood may be produced during the static and shrinking states to maintain the reduced allometry; new tissue is filled with labile carbon, thereby maintaining a small, but biologically significant, sapwood labile pool. Much of this labile carbon, however, is retranslocated during the next time step. In scenarios (ii) and (iv), however, the labile carbon pools cannot support A. rubrum’s maintenance demands, and the escalating deficit culminates in tree mortality (Figure 4B and D).

The coupling of allometries and labile and structural carbon dynamics provides a framework for modeling carbon allocation. The allocation solutions yield dynamic patterns...
(Figure 6), as one might expect of real trees based on $^{14}$CO$_2$ labeling studies (Coleman et al. 1995, Hansen et al. 1996, Scarascia-Mugnozza et al. 1999, Dickson et al. 2000). Labeling experiments suggest that shade enhances the fractional allocation of photosynthate to foliage (e.g., Souza and Válio 1999). Likewise, the ACGCA model predicts that $f_L$ increases during canopy closure as light interception decreases (Figure 6G), paralleled by an increase in $f_R$ (Figure 6H) to maintain the RA:LA allometry (Eq. (18A)). Why do $f_L$ and $f_R$ increase and $f_T$ decrease during periods of reduced light? The trunk does not lose structural mass, but some labile carbon must be allocated to leaves, roots and branches to replace senesced tissues, thereby maintaining the target (or reduced) allometry. Once these tissues are replaced, then the remaining labile carbon is allocated to growth of all compartments. By definition, $f_T = 0$ for unhealthy trees, even though real trees may allocate a trivial amount to the trunk to maintain minimal radial growth. Relative allocation of labile carbon to leaves (and roots) increases by 2.0–2.5 times when transitioning from a static to shrinking state during the closed canopy phase (Figure 6G and H). Turnover rates of leaves and fine roots are 20 times greater than those of coarse roots and branches (see $S_i$ values, Table 2). Thus, when $E$ is low (or light is low), substantially more labile carbon must be invested in leaves and fine roots compared to sapwood to maintain the reduced allometry.

**Gap dynamics scenarios and implications for real trees**

The ACGCA model yields a range of behaviors consistent with field and experimental observations. By design, the model produces modeled trees that look like real trees because it incorporates empirical allometries. The model also gives labile carbon economies that result in realistic tree behavior. For example, empirical studies have shown that labile carbon reserves are important to tree growth and survival in stressful environments (e.g., Chapin et al. 1990, Renaud and Mauffette 1991). Likewise, the model predicts that labile carbon is critical to survival during low-light stress that occurs during a closed canopy. Based on the simulations, *P. taeda* died during the first gap cycle in 50 of the 62 gap dynamics scenarios. The simulations associated with the greatest light stress (e.g., canopy closure time of 5 years) always caused mortality and indicated that *P. taeda* can only survive for about 2 years in the static and shrinking states before depleting its labile reserves. *Acer rubrum* can survive much longer on its reserves such that it died during the first gap cycle in only 28 of the 62 scenarios. For the scenarios with a 5-year canopy closure period, *A. rubrum*’s labile carbon reserves allowed it to survive 5–42 years in the static and shrinking states before dying. The lifetime of *A. rubrum*’s reserve pool depended on the open gap phase such that longer open gaps resulted in a larger labile carbon pool upon canopy closure, extending the life of the tree. In general, the simulation results are consistent with seedling defoliation experiments under different light levels, which indicate that species-specific abilities to tolerate shade are strongly tied to labile carbon (Canham et al. 1999, Gleason and Ares 2004).

Of the 12 scenarios for which *P. taeda* survived, all were defined by gradual canopy closure (i.e., canopy closure took 45 years). It also survived when canopy closure took 25 years, given that the gap return interval was 35 years (for 4-year open gap) or 35 or 50 years (for 6- and 8-year open gaps). This implies that *P. taeda* does well in open stands and that the seedling and sapling stages are most susceptible to low-light mortality. Once a tree becomes established under high light and continues to experience favorable light as it matures and develops a ‘large’ labile carbon pool, then as an adult, it is able to survive long periods of low light. On the other hand, of the 28 scenarios for which *A. rubrum* died, it always died when the time between gaps was 200 years. Consider the scenario where *A. rubrum* died and *P. taeda* survived (Figure 4B); both species entered the shrinking state near the time of complete canopy closure. At this time, *A. rubrum*’s excess labile carbon flux (i.e., $E$) was nearly 20 times greater than that of *P. taeda*, but it also had over five times the amount of leaf, fine root, and sapwood mass compared to *P. taeda*. With reduced carbon gain due to low-light conditions during closed canopy, the large amount of actively respiring tissue gradually reduced *A. rubrum*’s excess labile pool, eventually creating a carbon deficit and tree death. Gradual canopy closure allowed *P. taeda* to reach its maximum height before complete closure such that a part of its crown extended above the forest canopy. Thus, given that *P. taeda*’s respiratory demands were small compared to *A. rubrum*’s, it had access to sufficient light to maintain a positive carbon balance. Despite $E > 0$, *P. taeda* still did not bring in enough carbon to replace all senesced tissues and thus gradually shrank in size during the closed canopy period.

The contrasting growth patterns predicted for *A. rubrum* and *P. taeda* agree with empirical evidence indicating that these two species vary in their shade-tolerance and successional status (e.g., Baker and Langdon 1990, Walters and Yawney 1990). Shade-intolerant species such as *P. taeda* rapidly invade open areas during recovery from disturbance, such as following abandonment of agricultural fields (Billings 1938). The invasion success of *P. taeda* is attributed to its comparatively high seedling emergence, survival and growth under open-canopy conditions (Desteven 1991). As the stand fills in, *P. taeda* densities decrease, paralleled by an increase in shade-tolerant species such as *A. rubrum* (Billings 1938, Oosting 1942, Harcombe et al. 2002). A shift in dominance from, for example, *P. taeda* to *A. rubrum* has been attributed to their differential abilities to compete for light (Harcombe et al. 2002), especially at the seedling stage (e.g., Groninger et al. 1996). Compared to *A. rubrum*, *P. taeda* seedlings are very responsive to changes in light, exhibiting superior growth under direct sun but markedly inferior growth in shade (Groninger...
et al. 1996). Likewise, the ACGCA model predicts that (i) A. rubrum seedlings and saplings are more capable of surviving lengthy periods of low light, but (ii) the growth and survival of P. taeda is strongly affected by light such that it grows much faster in open gap conditions. Field studies also suggest that radial growth of mature P. taeda trees is dampened by moderately low light, whereas the growth of mature A. rubrum trees is apparently unaffected (McDowell and Urban 2004). Simulations support this such that P. taeda’s growth and physiological state are more sensitive to changes in light than A. rubrum, and A. rubrum is much more likely to survive repeated bouts of low light, as long as the closed-canopy period is disrupted by a gap-forming disturbance every 100 years or less. On the other hand, P. taeda is expected to persist if canopy closure is gradual, allowing trees to establish and become canopy dominants.

Conclusions

The ACGCA model is a semi-mechanistic framework for describing tree growth, allocation and mortality. The model captures a range of physiological states characteristic of real trees by coupling empirical allometries, simple physiology, and structural and labile carbon dynamics. Although the complete model contains a large number of equations, most describe simple mass–balance relationships, and many are derived from each other. For example, the equations associated with the living, nonhealthy physiological states are derived from the healthy state equations using a small number of rules. Additionally, the equations are constructed such that nearly all parameters are biologically meaningful (see Table 2) and can be estimated from field or laboratory data.

An important feature of the ACGCA model is its modular structure, facilitating straightforward modification of its components. The radiation-use model for carbon gain could be replaced with a more mechanistic one, and the allometries could be tailored to accommodate, for example, the effects of crowding on the H:D relationship (Henry and Aarsen 1999), size-dependent xylem tapering (Anfodillo et al. 2006, Weitz et al. 2006) or SA:LA ratios that vary with tree height (e.g., McDowell et al. 2002). We recognize that there are other carbon sinks (e.g., reproduction and root exudation) that are not currently considered given the limited information available to define and parameterize their dynamics. Future directions will incorporate such sinks and couple more realistic (yet more detailed) allometries to a semi-mechanistic photosynthesis model (e.g., Farquhar and von Caemmerer 1982, Katul et al. 2000) that includes stomatal regulation of CO2 exchange (e.g., Sperry 2000, Katul et al. 2003). Another goal is to obtain better parameter estimates by rigorously fitting the model to empirical data. Species-specific estimates will provide insight into the importance of variation in physiological, morphological and allometric traits for different shade-tolerance strategies. This is valuable because realistic predictions of forest succession and productivity require an understanding of the mechanistic basis of shade-tolerance. In this study, we showed that the ACGCA model provides a framework for using what we know, or can observe, about structural relationships to predict labile carbon dynamics. The model suggests that variation in labile carbon storage and allocation may underlie species differences in shade-tolerance strategies, plant performance and forest succession.

Supplementary Data

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

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