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**Article:**
A process-based model of conifer forest structure and function
with special emphasis on leaf lifespan

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Received 18 September 2001; revised 2 April 2002; accepted 16 May 2002; published 23 November 2002.

[1] We describe the University of Sheffield Conifer Model (USCM), a process-based approach for simulating conifer forest carbon, nitrogen, and water fluxes by up-scaling widely applicable relationships between leaf lifespan and function. The USCM is designed to predict and analyze the biogeochemistry and biophysics of conifer forests that dominated the ice-free high-latitude regions under the high $p$CO$_2$ “greenhouse” world 290–50 Myr ago. It will be of use in future research investigating controls on the contrasting distribution of ancient evergreen and deciduous forests between hemispheres, and their differential feedbacks on polar climate through the exchange of energy and materials with the atmosphere. Emphasis is placed on leaf lifespan because this trait can be determined from the anatomical characteristics of fossil conifer woods and influences a range of ecosystem processes. Extensive testing of simulated net primary production and partitioning, leaf area index, evaportranspiration, nitrogen uptake, and land surface energy partitioning showed close agreement with observations from sites across a wide climatic gradient. This indicates the generic utility of our model, and adequate representation of the key processes involved in forest function using only information on leaf lifespan, climate, and soils.

INDEX TERMS: 1615 Global Change: Biogeochemical processes (4805); 3337 Meteorology and Atmospheric Dynamics: Numerical modeling and data assimilation; 3344 Meteorology and Atmospheric Dynamics: Paleoclimatology; 9609 Information Related to Geologic Time: Mesozoic; KEYWORDS: leaf lifespan, conifer forests, vegetation model, paleoclimate, scaling mechanisms, forest-atmosphere fluxes


1. Introduction

[2] The current situation of glaciated polar regions surrounded by sparse, low-stature tundra is unusual in the geologic history of vascular land plants [Frakes et al., 1992]. The plant fossil record demonstrates that tall, productive, conifer forests covered the high latitude land-masses between the Permian and the Eocene, 290–50 million years (Myr) ago [Jefferson, 1982; Spicer and Parrish, 1986, 1990; Spicer and Chapman, 1990; Taylor et al., 1992]. These ancient polar forests provide tangible evidence for a major poleward advancement of the tree line, and flourished under a high $p$CO$_2$ [Crowley and Berner, 2001] and a warm, ice-free climate [Frakes et al., 1992], despite extended periods of continuous summer daylight and winter darkness [Read and Francis, 1992; Beerling and Osborne, 2002]. One of the most intriguing features of these ecosystems was the distinctive biogeography of their leaf habit, with a mixture of evergreen and deciduous species in Arctic forests, and evergreens predominating in Antarctica [Falcon-Lang, 2000a, 2000b; Falcon-Lang and Cantrill, 2000, 2001]. Contemporary evergreen and deciduous forests alter the seasonal course of vegetation-climate feedbacks, particularly at the regional scale [Bonan et al., 1992; Sellers et al., 1997; Betts et al., 1997; Levis et al., 1999; Douville et al., 2000]. The action of forest feedbacks on climate, through changes in land surface energy, moisture, and momentum fluxes, are especially strong in the mid- to high-latitude regions, and presumably operated in the distant past [Otto-Bliesner and Upchurch, 1997]. However, paleoclimatet modeling studies have tended to uncouple land-atmosphere energy exchanges from physiological processes and their responses to the global environment.

[3] Just how the polar climate influenced the biogeography of these ancient forests [Axelrod, 1966, 1984; Douglas and Williams, 1982; Creber and Chaloner, 1985] and how, in turn, the forests affected regional climates, continues to remain uncertain. Conifer forests are optically darker than other vegetation types, allowing them to absorb more solar radiation, with a greater potential for evaporating water and heating the air and soil [Jarvis et al., 1976]. They are also aerodynamically rougher, enhancing the transfer of mass and energy through increased turbulence. These feedback characteristics therefore represent a “miss-
New techniques in paleobotany [Falcon-Lang, 2000a, 2000b], and novel observations from global-scale plant physiological studies [Reich et al., 1992, 1997, 1998a, 1998b, 1999], now offer the potential to develop a new mechanistic approach for investigating these issues. In the paleobotanical realm, Falcon-Lang [2000a, 2000b] has established an important quantitative technique for determining leaf lifespan from cellular analyses of fossil conifer woods. His approach utilizes the inverse correlation between growth ring markedness (defined as the percentage of late wood and decline in cell size within a given ring) and leaf lifespan across a wide range of contemporary northern and southern hemisphere conifer taxa. Initial studies on tropical (2–13°C) Carboniferous gymnosperm woods and high latitude (72°C) early-Cretaceous fossil conifer woods indicate evergreen forests in both cases, in agreement with more traditional palaeobotanical approaches [Falcon-Lang and Cantrill, 2001]. Interestingly, leaf retention times of the Antarctic species were estimated to be 5–13 years, values approaching the upper limit in modern conifers [Chabot and Hicks, 1982].

Alongside these developments in paleobotany, Reich et al. [1992, 1997, 1998a, 1998b, 1999] reported, from a global set of observations, that leaf lifespan was strongly related to carbon uptake (by photosynthesis) and loss (by respiration), transpiration, and nutrient content. The relationships between leaf form, function, chemistry, and longevity are remarkably robust and hold for terrestrial plants with contrasting evolutionary and climatic histories [Reich et al., 1997]. In general, longer-lived leaves are mechanically tougher [Coley, 1988], have a lower nitrogen content, stomatal conductance, and rates of photosynthesis and

**Figure 1.** The functional consequences of an increase in leaf lifespan from the leaf to the ecosystem scale, as represented by the model. Numbers indicate the model equations describing leaf-scale relationships. Arrows linking boxes indicate interactions between processes at progressively larger scales. Arrows within boxes denote the direction of change in a process generally resulting from an increase (up arrow) in leaf lifespan.
respiration than their shorter-lived counterparts (Figure 1) [Reich et al., 1992, 1998a, 1998b, 1999]. These traits slow ecosystem cycling of carbon and nutrients by leading to high biomass canopies with longer residence times, and by retarding rates of soil nutrient release by litter decomposition (Figure 1) [Schlesinger, 1997]. Collectively, the functional interactions between leaf lifespan and key plant traits govern major components of conifer forest ecology and biogeochemistry, and offer great scope for numerically modeling these processes.

Building on this research, we describe a generic process-based model of conifer forest structure and function (University of Sheffield Conifer model, USCM), which emphasizes leaf lifespan through the fundamental relationships reported by Reich et al. [1992, 1998a, 1998b, 1999]. The objective of this paper is to examine the hypothesis that a conifer model, using leaf lifespan as the driving physiological variable, can explain large-scale distribution patterns of leaf area index and net primary productivity. The work is developed with the long-term research objective of reconstructing high-latitude forests that existed 290–50 Myr ago, and their interactions with the greenhouse climate that prevailed at the time.

2. Model Description

Our model focuses on the large-scale implications of variation in leaf lifespan (Figure 1), and is designed for application at scales ranging from local to global, both in the present and geologic past. Four important aspects of forest function and their coupling are considered in relation to leaf lifespan: carbon exchange with the atmosphere, fluxes of water through the soil-plant-atmosphere continuum, limitation of growth by nitrogen, and land surface-atmosphere energy exchange (Figure 2 and Table 1). Leaf lifespan is a key input to the model and is integrated so that its impacts on the carbon, nitrogen, water, and energy budgets cascade to progressively larger scales (Figure 1 and Table 1). Inclusion of leaf lifespan and conifer-specific environment responses provide a more direct means of scaling from fossil wood analyses [Falcon-Lang, 2000a, 2000b; Falcon-Lang and Cantrill, 2000, 2001] than might be achieved using generic global vegetation models [e.g., Cramer et al., 2001; McGuire et al., 2001].

2.1. Carbon Balance

The net primary productivity of vegetation $P_n$ is the annual balance between net canopy photosynthesis $A_c$ and respiration $R$. Respiration produces the energy for two main groups of processes, and these are divided for the purposes of modeling, although they share a number of biochemical pathways [Amthor, 2000]: first, the maintenance of existing plant tissues via the processes of repair, turnover, acclimation, and active transport $R_M$; secondly the growth of leaf bud, root tip, and woody cambium meristems, accounting for energy expended in the nutrient uptake and transport required
Table 1. Treatment of Ecosystem Physiology in the University of Sheffield Conifer Model (USCM)

<table>
<thead>
<tr>
<th>Physiology</th>
<th>Treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shortest time step</td>
<td>1 hour</td>
</tr>
<tr>
<td>Photosynthesis</td>
<td>enzyme-based [Farquhar et al., 1980], dependent on leaf lifespan</td>
</tr>
<tr>
<td>N uptake by vegetation</td>
<td>dependent on soil carbon and nitrogen status, and air temperature</td>
</tr>
<tr>
<td>Radiation</td>
<td>[Woodward et al., 1995]</td>
</tr>
<tr>
<td>Stomatal conductance</td>
<td>dependent on photosynthesis, leaf-to-air vapor pressure deficit,</td>
</tr>
<tr>
<td></td>
<td>atmospheric CO₂, soil moisture [Leuning, 1995; Woodward et al., 1995]</td>
</tr>
<tr>
<td>Canopy temperature</td>
<td>canopy energy balance [Monteith and Unsworth, 1990]</td>
</tr>
<tr>
<td>Aerodynamics</td>
<td>dependent on leaf area index and height [Shaw and Pereira, 1982]</td>
</tr>
<tr>
<td>Sapwood respiration</td>
<td>dependent on sapwood volume and temperature [Ryan et al., 1995]</td>
</tr>
<tr>
<td>Fine root respiration</td>
<td>dependent on nitrogen and temperature [Ryan et al., 1996]</td>
</tr>
<tr>
<td>Leaf area index</td>
<td>has to satisfy carbon, nitrogen, and water requirements</td>
</tr>
<tr>
<td>C allocation</td>
<td>annual using functional relationships with carbon, nitrogen, and water</td>
</tr>
<tr>
<td>N allocation</td>
<td>requirements</td>
</tr>
<tr>
<td>Evapotranspiration</td>
<td>dependent on leaf lifespan and fixed concentrations for wood and roots</td>
</tr>
<tr>
<td>Water balance</td>
<td>transpiration [Penman, 1948; Monteith, 1965] + interception</td>
</tr>
<tr>
<td>N-mineralization not explicitly simulated</td>
<td></td>
</tr>
</tbody>
</table>

...to supply these processes [Lambers et al., 1983]. Growth respiration is expressed as the efficiency of dry matter production from fixed carbon \( Y_G \) [Thornley, 1970], giving

\[
P_n = m_e Y_G \sum_{m=1}^{12} \left( A_e - R_M \right),
\]

where \( A_e \) and \( R_M \) are calculated for each month \( m \) to give an annual net carbon balance, and \( m_e \) converts moles of fixed carbon to mass of sugars.

[9] Net canopy photosynthesis \( A_c \) is simulated using a biochemical model of leaf photosynthesis, by treating sunlit and shaded fractions of the canopy as a “big-leaf” [Farquhar et al., 1980; de Pury and Farquhar, 1997]. Photosynthesis is sensitive to canopy temperature, incident solar radiation, and the diffusion of atmospheric CO₂ and O₂ into leaves. It is therefore closely coupled with both canopy energy balance and resistance to gaseous diffusion imposed by stomata (Figure 2). The impacts of leaf lifespan on these canopy processes are exerted through its relationship with photosynthetic capacity, respiration rate, stomatal conductance, and the mass:area ratio (Figure 1). The control of photosynthesis and respiration by leaf lifespan operates through its relationship with nitrogen content (Figure 1).

[10] Canopy photosynthesis is the sum of rates for sunlit \( A_s \) and shaded \( A_{sh} \) populations of leaves [de Pury and Farquhar, 1997], calculated for each hour of the day \( h \), and summed for the days in each month \( d \)

\[
A_c = d \sum_{h=1}^{24} 3600(A_s + A_{sh}).
\]

[11] The 3600 term integrates \( A_c \) from seconds to hours. Both \( A_s \) and \( A_{sh} \) depend on the balance between respiration \( R_d \) and CO₂ fixation, which is determined by either regeneration of the CO₂-accepting molecule Ribulose-1,5-bisphosphate (RubP) \( A_v \), or activity of the primary carboxylating enzyme RubP carboxylase/oxygenase (Rubisco) \( A_v \) [Farquhar et al., 1980]

\[
A = \min\{A_s, A_{sh}\} - R_d,
\]

where “\( \min \)” denotes “the minimum of.” Rubisco-limited photosynthesis is governed by: the partial pressures of CO₂ and O₂ within the leaf, \( C_i \) and \( O_i \), respectively; the enzyme’s temperature-sensitive affinities for these gases, \( K_c \) and \( K_o \), respectively [Bernacchi et al., 2001]; and its carboxylation capacity \( V_{c,\text{max}} \), such that

\[
A_v = V_{c,\text{max}} \frac{C_i - C_p}{C_i + K_c(1 + O_i/K_o)}.
\]

where \( C_p \) is the CO₂ compensation point [von Caemmerer, 2000]. Regeneration of RubP in the Calvin Cycle is limited by light-dependent electron transport \( J \), so that

\[
A_j = J\frac{(C_i - C_p)}{4C_i + 8C_p},
\]

where

\[
J = \frac{\phi Q}{\sqrt{1 + \phi^2 Q^2/J_{\text{max}}^2}}.
\]

The latter is an empirical function of the electron transport capacity \( J_{\text{max}} \), the quantum flux \( Q \) of photosynthetically active radiation (PAR) absorbed by canopy leaves, and the quantum efficiency of electron transport \( \phi \). Values of \( V_{c,\text{max}} \) and \( J_{\text{max}} \) are closely coordinated [de Pury and Farquhar, 1997]

\[
J_{\text{max}} = 2.1V_{c,\text{max}},
\]

but each responds independently to canopy temperature [Harley et al., 1992; Walcroft et al., 1997]. In addition to CO₂, O₂, and climate data, calculation of \( A_e \) therefore...
Table 2. Core Constants Distinguishing Conifers From Other Woody Species*  

<table>
<thead>
<tr>
<th>Constant</th>
<th>Value</th>
<th>Units</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a_s), Sensitivity of stomatal conductance to photosynthesis</td>
<td>28</td>
<td>mol H(_2)O</td>
<td>see Figure 3</td>
</tr>
<tr>
<td>(d_s, d_g), Empirical descriptors of the stomatal response to atmospheric vapor pressure</td>
<td>1199, 566</td>
<td>mmol(^{-1}) CO(_2) Pa</td>
<td>see Figure 3</td>
</tr>
<tr>
<td>(g_{lc}), Leaf cuticular conductance</td>
<td>3</td>
<td>mmol H(_2)O m(^{-2}) s(^{-1})</td>
<td>Körner [1994]</td>
</tr>
<tr>
<td>(H_k), Activation energy for respiration at 293 K ((l, s, r), coarse and ephemeral roots)</td>
<td>(l = 9593; s = 42850; r = 54110)</td>
<td>J mol(^{-1})</td>
<td>Walcroft et al. [1997], Ryan et al. [1995], and Murty et al. [1996]</td>
</tr>
<tr>
<td>(k_{ls}), Rate of decrease in leaf mass-to-area with canopy area</td>
<td>9.65</td>
<td></td>
<td>see Figure 3</td>
</tr>
<tr>
<td>(N_s), Sapwood nitrogen content</td>
<td>1.8</td>
<td>mg g(^{-1}) DM</td>
<td>Ryan [1991] and Gordon and Jackson [2000]</td>
</tr>
<tr>
<td>(N_{cr}), Coarse root nitrogen content</td>
<td>10.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(N_{e}), Ephemeral root nitrogen content</td>
<td>3.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(r_{s}), Volume-based root maintenance respiration rate</td>
<td>0.8</td>
<td>mmol CO(_2) mg(^{-1}) N s(^{-1})</td>
<td>Ryan et al. [1996]</td>
</tr>
<tr>
<td>(r_c), Leaf PAR absorptance</td>
<td>0.90</td>
<td>d’less</td>
<td>Gates [1979]</td>
</tr>
<tr>
<td>(\psi_s), Ephemeral fraction of roots</td>
<td>0.10</td>
<td>d’less</td>
<td>Gates [1979]</td>
</tr>
<tr>
<td>(\psi_l), Leaf PAR absorptance</td>
<td>0.25</td>
<td>d’less</td>
<td>Vogt et al. [1996]</td>
</tr>
<tr>
<td>(\Omega), Canopy clumping factor</td>
<td>0.55</td>
<td>d’less</td>
<td>Chen [1996], Chen and Black [1991], Chen et al. [1991], Foster et al. [1994], and Weis [2000]</td>
</tr>
</tbody>
</table>

*Notation: CH\(_2\)O, carbohydrate; DM, dry matter.

requires only an estimate of \(Q_s, V_{c,max}\), and \(R_d\) for each of the sunlit and shaded portions of the canopy.

[13] Canopy absorption of PAR is strongly influenced by the positioning of leaves, which are aggregated into whorls or clumps in conifers. This aggregation can be represented with a foliage-clumping index \(\Omega\) (Table 2), to estimate the canopy leaf area that is effective in intercepting radiation \(L_c\) [Chen and Black, 1992] from the actual leaf area index \(L_a\):

\[
L_c = \frac{\Omega L_a}{\chi}. \tag{8}
\]

[14] The mean \(\chi\) for ten species (Table 2) is defined as the ratio of \(L_c\) to \(L_a\), assessed experimentally using a combination of optical and destructive methods [Chen, 1996]. Vegetation cover \(\chi\) allows for incomplete coverage of the land surface by trees, and is calculated using the methods given by Betts et al. [1997]. Using \(L_c\) and \(\chi\), absorption of PAR by the whole canopy \(Q_c\), and its sunlit \(Q_s\) and shaded \(Q_{sh}\) fractions, each may be calculated on a land area basis following the study by de Pury and Farquhar [1997]:

\[
Q_c = \chi \int_0^{L_c} Q_b k_b (1 - \rho_s) \exp(-k_b L_s) dL + \chi \int_0^{L_c} Q_b k_{sh} (1 - \rho_s) \exp(-k_{sh} L_s) dL, \tag{9}
\]

and

\[
Q_{sh} = Q_c - Q_s. \tag{11}
\]

[15] The canopy extinction coefficients for beam and scattered PAR \(k_b\), diffuse and scattered PAR \(k_{ds}\), and beam PAR \(k_s\) vary with the solar zenith angle \(\theta\) [de Pury and Farquhar, 1997]. Similarly, the canopy reflection coefficients for beam PAR \(\rho_b\) and diffuse PAR \(\rho_d\) depend on \(\theta\) and leaf PAR absorptance \(\alpha_p\) (Table 2) [de Pury and Farquhar, 1997]. We estimate the incident beam \(Q_b\) and diffuse \(Q_d\) PAR using solar geometry and the empirical formulae of Weiss and Norman [1985], by assuming a well broken low cloud cover [Lumb, 1964].

[16] The vertical canopy profile of leaf physiological properties is derived from the area-based decline in nitrogen content \(N_c\) with depth in the canopy, and integrated to obtain \(V_{c,max}\) for sunlit \(V_s\) and shaded \(V_{sh}\) canopy fractions.
In a number of contrasting woody species, including conifers, the bulk of the decrease in leaf mass-to-area ratio, rather than any significant change in nitrogen concentration $N_l$ [Hollinger, 1989; Ellsworth and Reich, 1993; Rambal et al., 1996; Bond et al., 1999]. The leaf mass-to-area ratio $M_L$ declines at a constant rate with depth in the canopy (Figure 3), from a value in the uppermost leaf positions $M_0$ that correlates with $Z_l$ [Reich et al., 1999]:

$$M_L = M_0 - k_M L,$$  

where $M_L$ is the value of $M$ beneath a leaf area index of $L$, and $k_M$ is the rate of decrease, derived from observations of three conifer species with contrasting shade tolerance (Figure 3). Equation (12) was fitted by setting $M_0$ to the observed mean value of each species. The canopy profile of Rubisco carboxylation capacity $V_{m,max}$ tracks $M_L$:

$$V_{m,max} = \sigma_l V_m (M_0 - k_M L),$$  

where $V_m$ is the Rubisco carboxylation capacity on a foliage basis, and $\sigma_l$ accounts for the decline in $V_{m,max}$ with leaf age. Field evidence from a wide range of conifer species demonstrates a decline in photosynthetic capacity with leaf age, from a maximum shortly after full leaf

Figure 3. New model functions, based on field observations of contemporary species. The plotted line in each panel was obtained by fitting model equations to the published data shown as symbols. Equation numbers used in the text and the $r^2$ for fits are indicated for each. Upper left panel, the dependence of leaf in vivo carboxylation capacity $V_m$ on nitrogen content $N_l$ (equation (20)) using mean biome observations from Beerring and Quick [1995] and Reich et al. [1999]. Upper middle panel, the relationship between leaf dark respiration $R_m$ and $V_m$ (equation (23)), with mean biome observations from Reich et al. [1999]. Upper right panel, the decline in the leaf mass:area ratio $M_L$ with depth into the leaf canopy, as indicated by the overlying leaf area index $L$ (equation (12)): circles, *Pinus ponderosa*; squares, *Pseudotsuga menziesii*; triangles, *Tsuga heterophylla* [Bond et al., 1999]. Lower left panel, the correlation between stomatal conductance $g_s$ and net leaf photosynthesis $A$ (equation (34)) in 13 conifer species [Reich et al., 1999]. Lower middle panel, the relative decline in canopy stomatal conductance $f(D_a)$ with atmospheric vapor pressure deficit $D_a$ (equation (35)) resulting from stomatal closure in *Pinus pinaster* (triangles) and *Picea abies* (circles) canopies [Granier et al., 1996]. Lower right panel, the relative sensitivity of canopy stomatal conductance $f(w_a)$ to soil moisture availability $w_a$ (equation (36)), from the model of Granier and Loustau [1994], developed for *Pinus pinaster*. 

[de Pury and Farquhar, 1997]. In a number of contrasting woody species, including conifers, the bulk of the decrease in $N_l$ is attributable to a reduction in the leaf mass-to-area ratio, rather than any significant change in nitrogen concentration $N_l$ [Hollinger, 1989; Ellsworth and Reich, 1993; Rambal et al., 1996; Bond et al., 1999]. The leaf mass-to-area ratio $M$ declines at a constant rate with depth in the canopy (Figure 3), from a value in the uppermost leaf positions $M_0$ that correlates with $Z_l$ [Reich et al., 1999]:

$$M = M_0 - k_M L,$$  

where $M_L$ is the value of $M$ beneath a leaf area index of $L$, and $k_M$ is the rate of decrease, derived from observations of three conifer species with contrasting shade tolerance (Figure 3). Equation (12) was fitted by setting $M_0$ to the observed mean value of each species. The canopy profile of Rubisco carboxylation capacity $V_{m,max}$ tracks $M_L$:

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expansion to a minimum of around zero at leaf abscission [Reich et al., 1995]. This decline may be mechanistically linked with seasonal variation in soil nitrogen availability [Thornley, 1998]. However, it occurs continuously over several growing seasons in the case of an evergreen leaf [Reich et al., 1995], and is poorly correlated with nitrogen in some deciduous species [Wilson et al., 2000a], highlighting important uncertainty in the underlying mechanism. We therefore use the empirical factor $\sigma_v$, and integrate this important effect to the canopy scale by simulating a single cohort of leaves each year, which emerges from buds located throughout the canopy. For deciduous trees, the canopy $V_{c,max}$ declines from its maximum value to zero within a single growing season, giving

$$\sigma_v = \frac{(Z_i - t)}{Z_i}, \quad (15a)$$

where $t$ is the time elapsed since leaf budburst. The average canopy value of $\sigma_v$ for evergreens must account for multiple cohorts of leaves, each separated by a year in age

$$\sigma_v = (1 - \sigma_{min}) \frac{(Z_i - t)}{Z_i} + \sigma_{min}, \quad (15b)$$

where $\sigma_{min}$ is the minimum canopy value of $\sigma_v$, immediately before the flush growth of new leaves, given by

$$\sigma_{min} = \frac{Z_i - 12}{Z_i}. \quad (16)$$

[17] The values of $V_s$ and $V_{sh}$ are obtained by integrating equation (14) for sunlit and shaded canopy fractions as described by de Pury and Farquhar [1997]

$$V_s = \chi_s \sigma_s \int_0^{L_c} [V_m(M_0 - k_M L)]dL, \quad (17)$$

$$V_s = \chi_s \sigma_s \int_0^{L_c} [V_m(M_0 - k_M L)\exp(-k_0 L)]dL, \quad (18)$$

$$V_{sh} = V_c - V_s. \quad (19)$$

The value of $V_m$ is calculated from $N_1$ (Figure 3)

$$\log V_m = 2.22 \log N_1 - 3.28. \quad (20)$$

[18] The close correlation between these variables (Figure 3) was obtained using paired observations of mean photosynthesis and leaf nitrogen for eight diverse biomes [Reich et al., 1999], with $V_m$ calculated following the method of Beerling and Quick [1995]. Since $N_1$ is also correlated with leaf lifespan $Z_i$ [Reich et al., 1998a], canopy photosynthesis ultimately depends on this trait (Figure 1):

$$\log N_1 = 1.57 - 0.34 \log Z_i. \quad (21)$$

[19] Leaf respiration is sensitive to temperature and strongly inhibited by light [Atkin et al., 2000]. Although some evidence points to a direct repression of activity in key respiratory enzymes by elevated $p$CO$_2$, this remains controversial, and is not considered at present [Drake et al., 1999]. Leaf respiration is thus

$$R_d = r_T r_Q R_w, \quad (22)$$

where $R_w$ is $R_d$ under standard conditions of temperature and light. The response of $R_d$ to absorbed PAR $R_Q$ follows the work of Amthor [1994], and its temperature sensitivity $r_T$ is described by an Arrhenius response with an activation energy $H_L$ (Table 2) [Walcroft et al., 1997]. Values of $R_w$ for sunlit and shaded portions of the canopy are obtained by substituting $V_m$ with mass-based canopy dark respiration $R_m$ in equations (17–19). The relationship between $R_m$ and $N_i$ is similar to the correlation between $V_m$ and $N_i$ (equation (20)), because the turnover of nitrogen-rich proteins such as Rubisco is metabolically expensive [Reich et al., 1998b; Amthor, 2000]. Without compelling evidence for a shift in the balance between photosynthesis and respiration with leaf lifespan [D. S. Ellsworth, personal communication; Reich et al., 1998b, 1999], we adopted a direct relationship between $R_m$ and $V_m$ derived from mean observations for eight diverse biomes [Reich et al., 1999] (Figure 3)

$$R_m = 0.022V_m + 3.1. \quad (23)$$

[20] This method is supported by a mechanistic link between the energy requirements of Rubisco turnover and respiratory activity [Penning de Vries, 1975].

[21] Maintenance respiration of non-photosynthetic organs $R_M$ occurs largely in the roots $R_r$, and living cells of the sapwood $R_s$

$$R_M = d(R_r + R_s). \quad (24)$$

[22] Root respiration is sensitive to temperature and closely correlated with the nitrogen concentration in coarse $N_c$ and ephemeral $N_e$ roots (Table 2), because of a tight coupling between nitrogen, protein content, and metabolic activity [Ryan et al., 1996]

$$R_r = 24 \times 3600 \times r_T r_Q [N_c \phi_r + N_e (1 - \phi_r)] W_r \times 10^{-9}, \quad (25)$$

where $r_N$ is the sensitivity of respiration to root nitrogen content, $W_r$ is the total root mass, and $\phi_r$ is the fraction of $W_r$ comprising ephemeral roots (Table 2). The temperature-sensitivity of root respiration follows an Arrhenius response (Table 2). Field evidence suggests that root respiration is negligible during the period of winter dormancy [Striegel and Wickland, 1998], when physiological activity approaches a minimum. We therefore consider fine root respiration to be zero during leafless periods in deciduous trees.

[23] The maintenance respiration of sapwood is more closely related to its volume $v_s$ than nitrogen concentration $N_s$ [Ryan et al., 1995], giving

$$R_s = r_T r_Q v_s, \quad (26)$$

where $r_N$ is the respiration rate per unit sapwood volume (Table 2). The value of $v_s$ is estimated from tree height and
the cross-sectional area of sapwood [Osborne and Beerling, 2002].

The growth efficiency $Y_G$ is insensitive to environmental conditions, but differs between different plant tissue types according to their chemical composition (Table 2). It is weighted by $P_n$

$$Y_G = \sum_i \left[ \frac{P_n}{Y_i} Y_i \right],$$

where the subscript $i$ denotes leaves, roots, or sapwood, for $P_n$ or $Y_G$. The cost of leaf growth increases on an area basis because $M$ rises with lifespan (equation (13)), but the mass-based $Y_G$ remains unchanged [reviewed by Poorter and Villar, 1997]. Field evidence demonstrates that this occurs because a decline in energetically expensive proteins with lifespan is paralleled by a decrease in energetically cheap minerals [Poorter and de Jong, 1999].

### 2.2. Energy and Water Budgets

[25] Net radiation at the canopy $\Phi_c$ and soil $\Phi_s$ surfaces is dissipated by latent $\lambda E$, sensible $H$, and soil $G_s$ heat fluxes [Monteith and Unsworth, 1990]

$$\Phi_c + \Phi_s = \lambda E + H + G_s.$$  

[26] The influx of energy to the canopy from absorbed PAR $P_c$ and near infrared radiation (NIR) $N_c$ is calculated using equation (9), with appropriate values for leaf absorptance (Table 2). Downward flux of longwave radiation from the sky $L_d$ is an additional energy source, which varies with air and cloud temperature [Jones, 1992], and the cloud cover (assumed to be 50%). Longwave radiation is also emitted upward and downward $L_e$ from the canopy, and upward from the soil $L_s$, tracking the temperature of each according to Stefan’s Law [Monteith and Unsworth, 1990]. Net canopy radiation is thus

$$\Phi_c = P_c + N_c + L_d - 2L_e + L_s.$$  

[27] The value of $\Phi_s$ depends on PAR and NIR penetration of the soil and woody parts of trees, described by the absorptance of each, $\alpha_s$ and $\alpha_w$, respectively

$$\Phi_s = \alpha_s/\alpha_w \left[ \chi (1 - \alpha_w) + (1 - \chi) (P_1 - P_c + N_1 - N_c) + L_c - L_s \right].$$

[28] The soil warms during summer, and cools over the winter following observations [Williams et al., 1992], and we therefore approximate $G_s$ as 10% of $\Phi_s$ [Clothier et al., 1986], as an influx in summer and efflux in winter.

[29] Latent heat flux from a forest comprises transpiration by vegetation $\lambda E_i$, evaporation of rainfall intercepted by the leaf canopy $\lambda E_i$, and evaporation from the soil surface $\lambda E_s$. These are governed by physical properties of the atmosphere and water, aerodynamic characteristics of the vegetation, and stomatal conductance of the canopy [Penman, 1948; Monteith, 1965]

$$\lambda E_i = \frac{r \Phi_a + \rho_a c_p s g_s D_s}{s + \gamma} \quad I > 0,$$  

where $I$ is the quantity of precipitation $p$ intercepted by the canopy [Woodward, 1987] and $\beta$ is the ratio of actual to potential $\lambda E_s$, which increases with soil water content and wind speed [Chanzy and Bruckler, 1993], although the latter tends to be very low at the forest floor [Wilson et al., 2000b]. The aerodynamic conductance for evaporation from the forest floor $g_s$ [Jones, 1992] is estimated by assuming a roughness length of 0.01 m [Shuttleworth and Wallace, 1985] and wind speed of 0.4 m s$^{-1}$ at 1 m above the ground [Woodward, 1987]. The temperature dependences of $s$, the rate of change of saturation vapor pressure with temperature; $\gamma$, the psychrometer constant; $\rho_a$, the density of dry air; and $D_s$ are accounted for following Jones [1992].

[30] Total canopy conductance to water vapor flux $g_w$ comprises aerodynamic $g_a$ and stomatal $g_s$ conductance in series, by analogy with Ohm’s Law [Jones, 1992]. Aerodynamic properties of the canopy depend on: tree height; the density of foliage, as represented by $L_a$; the characteristic dimension of leaves; and wind speed, assumed to be 20 m s$^{-1}$ at 200 m above the ground [Shaw and Pereira, 1982; Jones, 1992; Woodward et al., 1995]. Stomatal conductance is correlated with photosynthetic rate and leaf lifespan [Reich et al., 1999], and regulated in response to atmospheric CO$_2$ partial pressure $C_a$, $D_a$, and soil water availability $w_a$ [Leuning, 1995]

$$g_{st} = g_{cut} + \frac{36.5 - C_p}{C_a - C_p} f(D_a) f(w_a) a_1 A,$$  

where $g_{cut}$ is on a molar basis [Woodward et al., 1995], $g_{cut}$ is the cuticular conductance, and $a_1$ the stomatal sensitivity to photosynthesis (Table 2 and Figure 3). The latter was fitted to paired values of $A$ and $g_s$ obtained from published measurements for 13 species of conifer in four biomes (Figure 3) [Reich et al., 1999]. The stomatal conductance in tree canopies declines with increasing $D_a$, following a well conserved relationship across a range of diverse species [Leuning, 1995; Granier et al., 1996]. This relationship (Figure 3) was fitted to observed values of stomatal conductance [Granier et al., 1996], obtained from sapflow measurements of water flux in two conifer species

$$f(D_a) = \frac{d_1}{d_1 + D_a},$$  

where $d_1$ and $d_2$ are fitted constants (Table 2). Chemical and hydraulic signals from the root system also induce stomatal closure in response to soil drying (Figure 3)

$$f(w_a) = 1 - s_1 \exp[s_2 w_a] + s_{\min},$$

where $s_{\min}$ is the minimum value of $f(w_a)$ in the field, while $s_1$ and $s_2$ are fitted constants (Table 2). The relationship describes the model of Granier and Loustau [1994], developed using sapflow measurements of the seasonal changes in canopy water fluxes during drought (Figure 3).
Values of $g_{SM}$ are calculated independently for sunlit and shaded populations of leaves by coupling with the photosynthesis model, and summed to obtain a whole-canopy conductance for the transpiration model.

[31] The balance between atmospheric $pCO_2$, photosynthetic $CO_2$ demand, and canopy conductance to the gas gives a value of $C_i$ for sunlit and shaded populations of canopy leaves

$$C_i = C_a - P \left( \frac{1.64 \times 10^4}{10^4 g_{SM}} \right),$$

where $P$ is the atmospheric pressure. Air temperature $T_a$ and the canopy exchange of sensible heat $H$ govern $T_e$ in an analogous manner [Monteith and Unsworth, 1990]

$$T_e = T_a + \frac{H}{\rho_c \phi_g \phi_a},$$

where $H$ is obtained by re-arranging equation (28)

$$H = \Phi_n + \Phi_s - \lambda E - G_s.$$

[32] These calculations of $T_e$ and $C_i$ allow the coupling of carbon, water, and energy flux models following a well established approach [Collatz et al., 1991]. Briefly: $A_s$ and $A_{sh}$ depend on $C_i$ and $T_e$; $g_s$ is sensitive to $A_s$ and $A_{sh}$; $\Phi_n$ is a function of $T_e$; $E_i$ is regulated by $\Phi_n$ and $g_s$; $T_e$ is determined by $\Phi_n$ and $E_i$; and $C_i$ by $A_s$, $A_{sh}$, and $g_s$. Osborne et al. [2000] describe this canopy-scale coupling in more detail.

2.3. Nitrogen Cycling

[33] The annual demand for nitrogen by vegetation $N_p$ is

$$N_p = 10^4 \sum_i N_{li} P_i,$$

where the subscript $i$ denotes values for leaves, roots, and sapwood. Re-translocation of the nutrient from senescing leaves to the meristems $N_t$ meets part of this demand, but the remainder must be extracted from the soil by root uptake $N_u$

$$N_p \leq (N_u + N_t).$$

[34] Mineral nitrogen availability is a primary limitation on plant growth in natural ecosystems because soil reservoirs are highly mobile, and regulated by the biological mineralization of organic matter [Vitousek and Howarth, 1991]. Increasing reliance on organic nitrogen in mineral-poor soils [Nasholm et al., 1998] reduces rates of plant nitrogen uptake and growth, requiring tighter symbiotic root associations with mycorrhizas [Read, 1990]. $N_u$ is therefore regulated by soil availability of the nutrient, and calculated by using soil carbon $S_c$ and nitrogen $S_{N}$ as indicators of soil organic matter and plant mycorrhizal status [Woodward and Smith, 1994a, 1994b]

$$N_u = \sum_{m=1}^{12} \left\{ 120d \min\{1, S_N/600\} \exp(-8 \times 10^{-5} S_C) \right\} \frac{P_t}{Z_t},$$

where $P_t$ is the net annual production of fine roots, and $Z_t$ their lifespan. We adopt the approach of Woodward et al. [1995] in accounting for the temperature-limitation of $N_u$, and the immobilization of organic matter by freezing.

[35] Re-translocation of nitrogen occurs principally from leaves, and this nitrogen recovery is correlated strongly with $N_t$ in both evergreen (equation (44a)) and deciduous (equation (44b)) species [Reich et al., 1992]

$$N_t = \frac{12 W_i}{Z_i} \left[ 0.585 N_t - 0.30 \right],$$

$$N_t = W_i \left[ 0.585 N_t - 0.30 \right],$$

where $W_i$ is the total leaf mass, obtained by integrating $M_L$ for the canopy $M_c$

$$M_c = \int_0^{L_c} \left[ M_0 - k_M L \right] dL.$$

[36] Thus the dependence of $N_t$ on $Z_t$ may be both direct (equation (44a)) and indirect, via its relationship with $M_L$ (equation (13)). Current evidence on the recovery of nutrients from senescent roots is conflicting [Ferrier and Alexander, 1991; Gordon and Jackson, 2000], and we have therefore adopted a conservative approach, with no significant root re-translocation [Gordon and Jackson, 2000].

2.4. Vegetation Structure

[37] The leaf area index $L_a$ is constrained by carbon, water, and nitrogen. First, $L_a$ must allow shaded leaves at the base of the canopy to maintain a positive annual carbon balance, after accounting for $Y_{Gl}$ [Woodward et al., 1995]. This carbon limitation of $L_a$ is thus dictated by canopy light penetration, leaf photosynthetic, and respiratory capacities. Secondly, $L_a$ is regulated so that the annual water consumption by plants matches the recharge of soil water by precipitation [Woodward, 1987]

$$E_{tot} \leq \sum_{m=1}^{12} (p - l),$$

[38] Long-lived leaves are more conservative in their water-use than short-lived leaves, having lower $g_s$ (Figure 1), with the potential to develop larger leaf canopies given the same water availability. Finally, the nitrogen required to produce new foliage must be met by root uptake (equations (41–43)); if not, $P_t$ is reduced and $P_e$ increased until this condition is satisfied. As with water-use, $L_a$ tends to increase with leaf lifespan because both $N_t$ and the fraction of the canopy replaced each year decline with $Z_t$, lowering canopy nitrogen requirements. Additionally, $L_a$ is constrained by $P_n$, which must be sufficient to meet $P_t$ after deductions for roots (equation (48)). Annual leaf production $P_l$ in evergreen (equation (47a)) and deciduous (equation (47b)) species is

$$P_l = \frac{12}{Z_t} L_a M_c,$$

$$P_l = L_a M_c.$$. 
without an explicit consideration of disturbance regimes, we would therefore expect to overestimate \( L_a \) in these ecosystems. By contrast, we underestimate \( L_a \) for sites dominated by a mixture of *Pseudotsuga menziesii* and *Tsuga heterophylla* in the Pacific Northwest (Figure 4). Field observations reveal that foliage in these deep forest canopies is more highly aggregated than in other conifers, with measurements yielding a clumping-index \( \Omega \) of 0.40, compared with the 0.55 used here (Table 2). Simulations with \( \Omega = 0.40 \) for these sites increase \( L_a \) in line with observations (Figure 4), markedly improving the regression between simulated and observed \( L_a \) (Figure 4, \( r^2 = 0.88 \)). This suggests that greater accuracy in USCM simulations of \( L_a \) for the geologic past might be obtained by estimating \( \Omega \) from fossil plant remains, particularly its needle-to-shoot area ratio component [Chen, 1996].

### 3.2. Net Primary Productivity (\( P_n \))

Simulations for \( P_n \) used the same leaf lifespan and soils data as the test for \( L_a \), but a climatology for the year matching observations. Across 19 sites, these showed a good correlation \((r^2 = 0.91)\) with observations (Figure 5), with no major systematic bias apparent across geographical regions or leaf lifespan (Figure 5). Agreement between observations and predictions indicates that the USCM realistically reproduces the interspecific and geographical variation in conifer productivity using only climatic, soil, and leaf lifespan information. We recognize that field observations, especially those of belowground productivity, are subject to significant uncertainty and so this test of our model is imperfect. Nevertheless, the observed errors are comparable to those of process-based vegetation models designed to predict the terrestrial biosphere response to future changes in pCO\(_2\), climate, atmospheric nitrogen deposition, and land use [Cramer et al., 2001; McGuire et al., 2001]. For these models, the published correlations between observed and predicted \( P_n \) are: \( r^2 = 0.95, n = 15 \) sites for the Sheffield Dynamic Global Vegetation Model described by Woodward et al. [1995]; \( r^2 = 0.72, n = 19 \) sites for the Integrated Biosphere Simulator, IBIS version 1.1 [Foley et al., 1996]; and \( r^2 = 0.74, n = 61 \) sites for Biome3 [Haxeltine and Prentice, 1996].

### 3.3. Carbon Partitioning, Transpiration, and Nitrogen Budgets

Four intensively studied reference sites in our database, indicated by asterisks in Table 3, were selected for testing plant carbon allocation between leaves, stems, and roots, leaf area index \((L_a)\), transpiration, and nitrogen uptake. These represent a diversity of leaf lifespans and climatic regimes, including boreal sites in Siberia and Canada, a southern US swamp forest and a site in the maritime Pacific Northwest (Table 3). All data were extracted directly from the sources given in Table 3, except annual ecosystem evapotranspiration which was compiled either from half-hourly average water vapor fluxes measured using eddy covariance [Chen et al., 2002; A. L. Dunn et al., BOREAS CO\(_2\) flux, temperature, and meteorological data, 2001 (available at http://www.as.harvard.edu/data/data.html) (hereinafter referred to as unpublished data, 2001)] or annual estimates [Kelliher et al., 1997; Liu et al., 1998].
### Table 3. Sites Used in Model Testing

<table>
<thead>
<tr>
<th>Location</th>
<th>Latitude Longitude</th>
<th>Climate Regime</th>
<th>Dominant Species</th>
<th>Zₚ</th>
<th>mths</th>
<th>MAT, °C</th>
<th>MAP, mm</th>
<th>Soil Cₑ</th>
<th>Soil Nₑ</th>
<th>Pₑ</th>
<th>m² g⁻¹ m⁻²</th>
<th>Lₑ</th>
<th>m²</th>
<th>Literature Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>Siberia</td>
<td>64°N 100°E</td>
<td>boreal</td>
<td><em>Larix gmelinii</em></td>
<td>4</td>
<td>7.3</td>
<td>-</td>
<td>443</td>
<td>10,900</td>
<td>638</td>
<td>83</td>
<td>20°</td>
<td>n/a</td>
<td>n/a</td>
<td>Kajimoto et al. [1999]</td>
</tr>
<tr>
<td>Siberia</td>
<td>61°N 128°E</td>
<td>boreal</td>
<td><em>L. gmelinii</em></td>
<td>4</td>
<td>8.9</td>
<td>-</td>
<td>399</td>
<td>10,900</td>
<td>638</td>
<td>104</td>
<td>4°</td>
<td>n/a</td>
<td>n/a</td>
<td>Schulze et al. [1995] and Kelliker et al. [1997]</td>
</tr>
<tr>
<td>Alaska</td>
<td>65°N 148°W</td>
<td>boreal</td>
<td><em>Pinus sylvestris</em></td>
<td>84</td>
<td>-3.7</td>
<td>-</td>
<td>493</td>
<td>2000</td>
<td>150</td>
<td>149</td>
<td>2.4°</td>
<td>n/a</td>
<td>n/a</td>
<td>Schulze et al. [1999] and Wirth et al. [1999]</td>
</tr>
<tr>
<td>Alaska</td>
<td>64°N 148°W</td>
<td>boreal</td>
<td><em>P. sylvestris</em></td>
<td>132</td>
<td>-2.4</td>
<td>-</td>
<td>304</td>
<td>11,000</td>
<td>735</td>
<td>220</td>
<td>3°</td>
<td>n/a</td>
<td>n/a</td>
<td>McGuire et al. [1992]</td>
</tr>
<tr>
<td>Canada</td>
<td>56°N 98°W</td>
<td>boreal</td>
<td><em>P. mariana</em></td>
<td>138</td>
<td>-1.9</td>
<td>-</td>
<td>501</td>
<td>15,000</td>
<td>980</td>
<td>243</td>
<td>4.1°</td>
<td>n/a</td>
<td>n/a</td>
<td>Gower et al. [1997], Steele et al. [1997] and Dunn et al. (unpublished data, 2001)</td>
</tr>
<tr>
<td>Germany</td>
<td>50°N 12°E</td>
<td>cool temperate</td>
<td><em>Picea abies</em></td>
<td>132</td>
<td>9.1</td>
<td>671</td>
<td>12,100</td>
<td>626</td>
<td>518</td>
<td>5.0</td>
<td>5°</td>
<td>n/a</td>
<td>n/a</td>
<td>Schulze et al. [1999]</td>
</tr>
<tr>
<td>Pacific NW</td>
<td>45°N 124°W</td>
<td>cool temperate</td>
<td><em>Picea sitchensis</em></td>
<td>48</td>
<td>10.2</td>
<td>1581</td>
<td>24,000</td>
<td>1210</td>
<td>669</td>
<td>5.3</td>
<td>5°</td>
<td>n/a</td>
<td>Gholz [1982] and Runyon et al. [1994]</td>
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</tr>
<tr>
<td>Pacific NW</td>
<td>45°N 123°W</td>
<td>cool temperate</td>
<td><em>Pseudotsuga menziesii</em></td>
<td>36</td>
<td>11.2</td>
<td>1095</td>
<td>24,000</td>
<td>1210</td>
<td>737</td>
<td>6.0</td>
<td>5°</td>
<td>n/a</td>
<td>Gholz [1982] and Runyon et al. [1994]</td>
<td></td>
</tr>
<tr>
<td>Pacific NW</td>
<td>45°N 122°W</td>
<td>cool temperate</td>
<td><em>P. menziesii</em></td>
<td>36</td>
<td>9.0</td>
<td>2300</td>
<td>24,000</td>
<td>1210</td>
<td>n/a</td>
<td>8.6</td>
<td>5°</td>
<td>n/a</td>
<td>Thomas and Winner [2000] and Chen et al. [2002]</td>
<td></td>
</tr>
<tr>
<td>Pacific NW</td>
<td>44°N 122°W</td>
<td>cool temperate</td>
<td><em>P. menziesii</em></td>
<td>36</td>
<td>7.3</td>
<td>1604</td>
<td>24,000</td>
<td>1210</td>
<td>530</td>
<td>n/a</td>
<td>5°</td>
<td>n/a</td>
<td>Grier and Logan [1977] and Sollins et al. [1980]</td>
<td></td>
</tr>
<tr>
<td>France</td>
<td>45°N 1°W</td>
<td>Mediterranean</td>
<td><em>Tsuga heterophylla</em></td>
<td>36</td>
<td>11.0</td>
<td>1411</td>
<td>24,000</td>
<td>1210</td>
<td>1077</td>
<td>8.7</td>
<td>5°</td>
<td>n/a</td>
<td>Runyon et al. [1994]</td>
<td></td>
</tr>
<tr>
<td>France</td>
<td>44°N 1°W</td>
<td>Mediterranean</td>
<td><em>P. pinaster</em></td>
<td>48</td>
<td>12.8</td>
<td>955</td>
<td>8300</td>
<td>645</td>
<td>n/a</td>
<td>6.0</td>
<td>5°</td>
<td>n/a</td>
<td>Granier and Loustou [1994]</td>
<td></td>
</tr>
<tr>
<td>France</td>
<td>43°N 5°E</td>
<td>Mediterranean</td>
<td><em>Pinus pinea</em></td>
<td>24</td>
<td>14.1</td>
<td>931</td>
<td>4150</td>
<td>322</td>
<td>688</td>
<td>n/a</td>
<td>5°</td>
<td>n/a</td>
<td>Rapp and Cabanettes [1981]</td>
<td></td>
</tr>
<tr>
<td>Israel</td>
<td>32°N 5°E</td>
<td>Mediterranean</td>
<td><em>Pinus halepensis</em></td>
<td>36</td>
<td>19.4</td>
<td>576</td>
<td>8300</td>
<td>645</td>
<td>n/a</td>
<td>2.5</td>
<td>5°</td>
<td>n/a</td>
<td>Schiller and Cohen [1995]</td>
<td></td>
</tr>
<tr>
<td>Southern US</td>
<td>36°N 79°W</td>
<td>warm temperate</td>
<td><em>Pinus taeda</em></td>
<td>30</td>
<td>15.7</td>
<td>1247</td>
<td>2558</td>
<td>147</td>
<td>1521</td>
<td>3.7</td>
<td>5°</td>
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<td>Kinerson et al. [1977] and Katal et al. [1999]</td>
<td></td>
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<tr>
<td>Southern US</td>
<td>36°N 76°W</td>
<td>warm temperate</td>
<td><em>Taxodium distichum</em></td>
<td>6</td>
<td>15.8</td>
<td>1279</td>
<td>15,000</td>
<td>1600</td>
<td>999</td>
<td>n/a</td>
<td>5°</td>
<td>n/a</td>
<td>Megonigal and Day [1988]</td>
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<tr>
<td>Southern US</td>
<td>31°N 82°W</td>
<td>warm temperate</td>
<td><em>T. distichum</em></td>
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<td>20.0</td>
<td>1260</td>
<td>15,000</td>
<td>1600</td>
<td>269</td>
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<td>5°</td>
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<td>Schlesinger [1978] and Liu et al. [1998]</td>
<td></td>
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<tr>
<td>Southern US</td>
<td>30°N 90°W</td>
<td>warm temperate</td>
<td><em>T. distichum</em></td>
<td>6</td>
<td>20.4</td>
<td>1561</td>
<td>15,000</td>
<td>1600</td>
<td>539</td>
<td>n/a</td>
<td>5°</td>
<td>n/a</td>
<td>Connor and Day [1976]</td>
<td></td>
</tr>
</tbody>
</table>

*Details for each of its geographical location, latitude and longitude, climatic zone, dominant species, leaf lifespan (Zₚ), and observations of leaf area index (Lₑ), and net primary productivity (Pₑ) with literature sources. Climatic and soils data inputs are summarized by mean annual temperature (MAT), mean annual precipitation (MAP), soil carbon, and nitrogen contents for each. n/a = data not available.

1 Soil carbon and nitrogen data from the study of Woodward and Smith [1994b] or Gower et al. [1997, 2000].

2 Productivity values either: °aboveground growth; or °total production.

3 Leaf area indices either: °actual (Lₑ) determined by destructive or allometric methods; or °effective (Lₑ) determined by an optical method.

4 Reference sites used in Figures 6–9. Where more than one location is listed for a given type of forest, we used data from the additional sources given for nearby sites.
Simulated partitioning of $P_n$ between leaves ($P_l$) and wood ($P_s$) closely matches observations at all four sites (Figure 6). Predictions of root production ($P_r$) show some discrepancies with observations for sites in Siberia and the Pacific Northwest (Figure 6). For the Siberian site, overestimation of $P_r$ may arise because we assume a complete annual turnover, whereas observations suggest root life-spans exceeding 20 years [Kajimoto et al., 1999]. In the case of the Pacific Northwest forests, $P_r$ was determined [Raich and Nadelhoffer, 1989; Runyon et al., 1994] by correlation with aboveground litter production for other vegetation types, a procedure likely to introduce some error into the estimate.

We acknowledge that the physiological mechanisms underpinning carbon allocation in plants are inadequately understood at present [Woodward et al., 1995; Woodward and Osborne, 2000]. However, this model test, undertaken at the four reference sites, demonstrates that our scheme of medium complexity, based on the functional requirements of leaves and roots [Givnish, 1986], provides a realistic approximation to observations in forests (Figure 6). A similar scheme successfully describes shoot and root allocation for forests along productivity gradients at the global scale [Friedlingstein et al., 1999]. We therefore regard it as adequate for our modeling purposes.

At the canopy scale, simulations of $L_a$ for each forest type closely reproduce observations (Figure 6), supporting the general applicability of the relationships between canopy productivity and leaf area (equations (12) and (13)). Accurate representation of $L_a$ in the USCM is important in

Figure 4. Leaf area index $L_a$. Upper panel, simulated values are compared to observations in conifer forests from a range of geographical regions, distinguished by different symbols (Table 3). The solid line shows exact agreement, while the dashed line is a regression of simulated values against observations with $r^2 = 0.63$. Lower panel, as upper panel, using a clumping factor value of 0.40 for sites where dominant vegetation is a mixture of Pseudotsuga menziesii and Tsuga heterophylla (see text for details). Regression is improved so that $r^2 = 0.88$.

Simulated partitioning of $P_n$ between leaves ($P_l$) and wood ($P_s$) closely matches observations at all four sites (Figure 6). Predictions of root production ($P_r$) show some discrepancies with observations for sites in Siberia and the Pacific Northwest (Figure 6). For the Siberian site, overestimation of $P_r$ may arise because we assume a complete annual turnover, whereas observations suggest root life-spans exceeding 20 years [Kajimoto et al., 1999]. In the case of the Pacific Northwest forests, $P_r$ was determined [Raich and Nadelhoffer, 1989; Runyon et al., 1994] by correlation with aboveground litter production for other vegetation types, a procedure likely to introduce some error into the estimate.

We acknowledge that the physiological mechanisms underpinning carbon allocation in plants are inadequately understood at present [Woodward et al., 1995; Woodward and Osborne, 2000]. However, this model test, undertaken

Figure 5. Net primary productivity $P_n$. Upper panel, simulated values are compared to observations in conifer forests from a range of geographical regions, distinguished by different symbols (Table 3). The solid line shows exact agreement, while the dashed line is a regression of simulated values against observations with $r^2 = 0.91$. Lower panel, difference between simulated and observed $P_n$ values by region. Positive values indicate overestimation by the model.
simulations of vegetation-climate feedbacks in high-latitudes, because it influences albedo, surface roughness, and the partitioning of energy fluxes at the land surface. Evapotranspiration is also important in this context, integrating the effects of canopy structure, climate, and stomatal physiology. For this variable, simulated values for all sites fall within the 20% range of uncertainty inherent in eddy covariance measurements (Figure 6), arising from missing data, instrument error, variation in the terrain, and meteorological conditions [Goulden et al., 1996; Moncrieff et al., 1996].

Nitrogen availability for growth, the sum of root uptake, and re-translocation from senescing tissues, is well described by the USCM (Figure 6), and is important because it frequently limits productivity in conifer forests [Bonan and van Cleve, 1992; Schulze et al., 1999]. Some of the small differences between predicted and observed nitrogen fluxes may be associated with the assumption of constant nitrogen concentrations for roots and sapwood (N_r and N_s, Table 2). It is possible that errors in observations, caused by the difficulty in estimating nitrogen re-translocation from long-lived foliage, also contribute to this discrepancy [Gower et al., 2000].

3.4. Partitioning of Energy Fluxes

Realistic representation of energy exchange between the forested land surface and the surrounding atmosphere is an essential component of the biogeophysical effects of vegetation on climate [Bonan et al., 1995], and therefore an important element of the model to examine. We tested predictions of the land surface energy balance over the boreal landscape, and its partitioning between fluxes associated with evapotranspiration (latent heat), sensible heat, net radiation, and soil heat flux, with data reported from the Boreal Ecosystem-Atmosphere Study [Sellers et al., 1995; A. L. Dunn et al., unpublished data, 2001]. Although other sites have also been subject to similar intensive measurement campaigns, these data are not yet available. For this test, the USCM was forced with observations of monthly climate (temperature, precipitation, and humidity). It reproduces with reasonable accuracy the seasonal course of net radiation, latent, and sensible heat fluxes shown by field measurements for the Canadian boreal forest (Figure 7). Moreover, the magnitude of all three terms is in general agreement with observations, indicating a suitable treatment of the land surface energy balance. Since we have independently validated predictions of canopy structure and transpiration (Figure 6), this result supports our scheme for energy balance, canopy aerodynamics, and conductance.

4. Model Sensitivity Analyses

4.1. Northern Hemisphere Simulations of Leaf Area Index (L_a) and Productivity (P_n)

We evaluated the effects of leaf lifespan on northern hemisphere patterns of L_a and P_n to assess the sensitivity of the USCM to large-scale variation in climate and soil properties. Analyses were restricted to the northern hemisphere because it encompasses the most extensive distributions of contemporary conifers [Olson et al., 1983]. Simulations were performed with leaf lifespans of 6 months (deciduous habit) and 120 months (evergreen habit), repre-
senting the extremes shown by modern conifers (Table 3). The results are not intended to reflect actual or potential contemporary vegetation patterns, which are determined by climatic extremes and competition between life forms [Woodward, 1987]. Instead they allow assessment of model sensitivity for contrasting lifespans to a wider range of climate and edaphic conditions than represented by the reference sites (Table 3). We forced the model with interpolated sets of global climate observations averaged for the period 1961–1990 [New et al., 1999, 2000], an atmospheric $pCO_2$ of 35 Pa and soil carbon and nitrogen contents from an interpolated global data set [Global Soil Data Task, 2000].

Figure 8 displays the broad-scale geographical patterns of $P_n$ and $L_a$ resulting from the prescription of two leaf lifespans throughout the Northern Hemisphere. These reflect climatic variations (precipitation, humidity, and land surface temperature) and differences in soil nutrient availability, and are in general agreement with the simulations of global vegetation models [Woodward et al., 1995; Foley et al., 1996; Cramer et al., 1999], indicating consistency between the alternative approaches.

Trees with short-lived leaves show greater variability in $L_a$ than those with longer-lived leaves (Figure 8), because they have a higher nitrogen and carbon cost of annual canopy replacement (equations (41) and (47a)), making $L_a$ more sensitive to climate and soil nutrient uptake. Despite this, the deciduous habit leads to a marginally greater $L_a$ (by 1–1.5 m$^2$ m$^{-2}$), by achieving higher photosynthetic rates under temperate conditions with adequate water and soil nutrients. Two exceptions to this general trend are apparent. First, in high-latitudes, where low temperatures limit soil nutrient supply and the length of the growing season. Secondly, in the dry tropics typical of modern savannahs and steppe vegetation [Mueller, 1982], where the long leaf lifespan achieves a higher $L_a$ than its shorter-lived counterpart because its stomatal conductance to water vapor are lower (Figure 1) and water-use is more efficient.

Simulated spatial patterns of $P_n$ for leaf lifespans of 6 and 120 months are similar and tend to track those of $L_a$ (Figure 8). The shorter lifespan results in a higher $P_n$ (by up to 200 g C m$^{-2}$ yr$^{-1}$) because higher leaf nitrogen contents (equation (21)) lead to higher maximum photosynthetic rates (equation (20)), when soil nitrogen content is adequate for the annual demand. As for $L_a$, the exception to these trends occurs in the high latitudes, but is more extensive in low latitude areas throughout equatorial South America and Africa, as well as southern and southeast Asia (Figure 8).

Evergreen vegetation is more productive in these aseasonal, moist tropical regions because the capacity of deciduous trees to exploit the environment is constrained by a short leaf lifespan. All of these differences follow the well-characterized global ecological contrasts between evergreen and deciduous trees [Chabot and Hicks, 1982; Schulze, 1982; Hollinger, 1992], indicating that the USCM may be of use for investigating the climatic and edaphic controls on the leaf habit of modern vegetation.

4.2. Sensitivity to Atmospheric $CO_2$, Climate Warming, and Solar Energy

Our model has been designed for analyzing polar forest biogeography and biogeochemistry between 290 and 50 Myr ago. It should therefore include appropriate sensitivity to a variety of past environmental conditions. Critical among these are $CO_2$, climate, and solar energy, which influence plant processes from the scale of individual leaves to whole ecosystems [Beerling, 1994, 1997, 2000]. Long-term carbon cycle models [Berner and Kothavala, 2001] and isotopic evidence from fossil soils [Ekart et al., 1999] indicate $pCO_2$ levels several times higher than current ambient during past greenhouse episodes [Crowley and Berner, 2001]. Additionally, many of these episodes are characterized by intense volcanic activity resulting from continental rifting. Volcanism itself exerts an influence on atmospheric $CO_2$ in the short-term [McElwain et al., 1999; Jones and Cox, 2001; Beerling, 2002], and on the quality of incoming solar radiation, as seen following the ejection of aerosols by the eruptions of El Chichon in 1982 and...
Leaf area index 
(m² m⁻²)

Lifespan = 6 months

Net primary productivity 
(g C m⁻² yr⁻¹)

Lifespan = 120 months

Difference (6 months - 120 months)
Mount Pinatubo in 1991 [Olmo et al., 1999]. Instrumental records showed attenuation of direct, and enhancement of diffuse, solar radiation, and a peak global cooling of 0.4 K after the Pinatubo eruption [McCormick et al., 1995]. Coupled ocean-atmosphere climate simulations of this event, with an interactive carbon cycle, indicate an impact of the cooling on the terrestrial biosphere, with significant net uptake of carbon by ecosystems in the tropics, but no major variations in oceanic carbon cycling [Jones and Cox, 2001].

We therefore performed a series of model experiments assessing the sensitivity of $P_n$ at our four reference sites (Table 3) to a rise in atmospheric $p_{CO_2}$ from 30 to 100 Pa, a range representing variations over the past 100 Myr [Ekart et al., 1999; Berner and Kothavala, 2001]. At each site, three experiments were performed to simulate episodes of global warming and volcanism: “control,” using unmodified climate; “warming,” with a 4.8 K rise in mean monthly temperature; “warming” + an “aerosol” term, defined from observations [Olmo et al., 1999] as a 10% reduction in direct and 33% enhancement of diffuse solar radiation. This change in the quality of solar radiation has little impact on total radiation, which changes by less than ±5% depending on $q$. The 4.8 K warming is equivalent to the radiative forcing effect from an increase in $p_{CO_2}$ to 100 Pa, calculated according to the method described by Kothavala et al. [1999]. Reductions in temperature following volcanic eruptions have not been investigated in this sensitivity analysis because they are within the range of uncertainty for paleotemperature proxies [Crowley and North, 1991].

A rise in atmospheric $p_{CO_2}$ increases $P_n$ in an asymptotic manner at all sites (Figure 9). However, the asymptote differs between sites, with stimulation of $P_n$ between 35 and 60 Pa $p_{CO_2}$ of 28% in the southern US forest, 38% in Siberia, 45% in the Pacific Northwest, and 56% in Canada (Figure 9). In support of the predicted $P_n$ increase for the southern US forest, we note that DeLucia et al. [1999] reported a 25% stimulation in a young Pinus taeda plantation in the Duke Forest after two years’ free-air $CO_2$ enrichment to 56 Pa. With a warming, $P_n$ increased further for any given $p_{CO_2}$ at all sites (Figure 9). As yet, no information has been reported from similar experiments with $CO_2$ enrichment and warming applied together, but other vegetation modeling studies support our findings for boreal conifer forests [Beerling et al., 1997; White et al., 2000].

In the USCM, the $CO_2$ response of $P_n$ is mediated by the net effect of several interacting factors. Rising $p_{CO_2}$ competitively inhibits the oxygenase activity of Rubisco and relieves substrate limitation of photosynthesis [Drake et
an effect on the atmospheric CO₂ record [Roderick et al., 2001], and occurs in addition to the large decline in global respiration and smaller decrease in tropical gross primary production induced by surface cooling [Jones and Cox, 2001; Rustad et al., 2001]. For the Pacific Northwest site, enhancement of diffuse radiation increases \( P_n \) by 1 m² across all \( pCO_2 \) values, leading to higher maintenance respiration costs of this already deep canopy under the mild winter climate of the region, and a net decrease in \( P_n \) ("warming + aerosols," Figure 9).

At present, the simulated response of \( P_n \) to these environmental perturbations excludes any feedback between plant litter and soil nutrient status [Bonan and van Cleve, 1992], a feature shown to be important in CO₂-enrichment experiments with conifer forests [Oren et al., 2001]. Changes in \( P_n \) and leaf lifespan affect the quantity and quality of surface litter and roots, key controls over rates of nutrient cycling through their effects on soil organic matter dynamics [Raich et al., 1991; Schlesinger, 1997; Parton et al., 1998]. Leaf lifespan is strongly linked with the rate of decomposition because trees with long-lived foliage produce recalcitrant litter, slowly releasing nutrients over long periods and ultimately generating a nutrient-poor soil. Leaves with a long lifespan are well adapted for such a soil, and their persistence is encouraged via this positive feedback [Aerts, 1995]. A major future development of our model will therefore be its coupling with a model of soil carbon and nitrogen dynamics [e.g., Raich et al., 1991; Parton et al., 1998].

5. Conclusions

Ever since the important recognition, nearly a century ago, that the polar regions were once covered by forests [Halle, 1913; Nathorst, 1914; Seward, 1914] debate has continued regarding the nature of their interaction with climate, especially survival during the mild, dark polar winters of the Mesozoic [Douglas and Williams, 1982; Chaloner and Creber, 1989]. Furthermore, the question of how the biogeochemical and biophysical characteristics of these unusual forests influenced regional climate in an ancient high CO₂ “greenhouse” world remains uncertain. To address these issues in a predictive, quantitative manner, we designed a process-based model of conifer function and structure, emphasizing the influence of leaf lifespan and its interactions with the environment.

Overall, a wide range of simulated vegetation properties validated well against observations from different taxonomic groups (Abies, Larix, Picea, Pinus, Pseudotsuga, Taxodium, Tsuga) with varying geographical ranges [Olson et al., 1983], indicating adequate representation of conifer functioning. We recognize that uncertainty exists regarding whether the plant-environment relationships seen in modern conifers are applicable to those growing in the distant past. However, the discovery of general leaf trait relationships across diverse terrestrial ecosystems, for plants with different evolutionary histories [Reich et al., 1997], provides the most secure basis yet for dealing with this issue.

The model can be used in a stand-alone mode to reconstruct polar forest properties at specific sites, based on leaf lifespan estimates from fossil woods [Falcon-Lang et al., 1997]. The stronger increase of \( P_n \) with \( pCO_2 \) at higher temperatures results from the synergistic interaction of these environmental variables on the photosynthetic system [Long, 1991]. A feedback also operates between the stimulation of \( P_n \) by \( pCO_2 \) and carbon allocation to roots. As \( P_n \) increases, there is an associated rise in the demand for nitrogen, which is met by a proportional increase in root respiration costs and turnover.

\[ CO_2 \text{-saturated } P_n \text{ values for all but the southern US site are constrained by the mean annual temperature (Figure 10), highlighting the significance of synergism between } pCO_2 \text{ and temperature. Imposition of warming in our model simulations shifts the } CO_2 \text{-saturated } P_n \text{ so that all follow a common trajectory given the prescribed soil characteristics, matching experimental evidence [Rustad et al., 2001]. At the southern US swamp forest site, annual demand by the deciduous canopy for nitrogen in high } pCO_2 \text{ outstrips the rate of uptake from the carbon-rich soil, where the decomposition of organic matter is retarded by a high water table [Schlesinger, 1978]. When this constraint is alleviated, } CO_2 \text{-saturated } P_n \text{ rises to conform with the temperature-limited rates of other sites (Figure 10), demonstrating the importance of coupling the above- and below-ground nitrogen cycles [cf. Bonan and van Cleve, 1992].}

\[ \text{The simulated effect of an increase in diffuse relative to direct radiation was typically an enhancement of } P_n \text{ ("warming + aerosols," Figure 9), due to enhanced and more uniform light penetration into the leaf canopy, resulting in more efficient photosynthetic } CO_2 \text{ uptake [Roderick et al., 2001]. This increase in } P_n \text{ could strengthen the terrestrial carbon sink following volcanic eruptions, with}

Figure 10. Relationship between \( CO_2 \)-saturated net primary productivity \( P_n \) determined from the “control” and “warming” scenarios (Figure 8) and mean annual temperature for the four reference sites. Arrows to broken lines indicate the effects of alleviating constraints on nitrogen uptake rate by decomposition at the Southern US swamp site (text for details). Values in brackets are leaf lifespan for the dominant species (Table 3).
and Cantrill, 2000, 2001] and paleoclimatic information from climate model simulations. Some aspects of these simulations, such as $F_n$ or the calculation of tree height from hydraulic considerations [Osborne and Beerling, 2002], can be compared with detailed studies of exceptionally well preserved in situ fossil forests [Francis, 1986, 1988]. More significantly, the next stage of development will be the coupling of above- and below-ground carbon and nitrogen cycles and the production of a conifer forest dynamics scheme using the simulated structure and function of trees with different leaf lifespans [Shugart, 2000]. The fully coupled USCM will then allow us to resolve detailed distributions of ancient high-latitude forests, and investigate the underlying climatic and biogeochemical controls on their biogeography, as well as their influence on regional climates.

**Notation**

- $A$: net photosynthesis ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$).
- $A_c$: rate of CO$_2$ fixation permitted by RuBP-regeneration ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$).
- $A_i$: A for the sunlit population of leaves in the canopy ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$).
- $A_{sh}$: A for the shaded population of leaves in the canopy ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$).
- $A_s$: rate of CO$_2$ fixation allowed by the activity of Rubisco ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$).
- $a_1$: sensitivity of $g_{sM}$ to $A$ (mol H$_2$O mmol$^{-1}$ CO$_2$) (Table 2).
- $C_a$: atmospheric partial pressure of CO$_2$ (Pa).
- $C_l$: partial pressure of CO$_2$ in leaf intercellular air spaces (Pa).
- $C_p$: CO$_2$ compensation point for photosynthesis (Pa).
- $c_p$: the specific heat capacity of water (1012 J kg$^{-1}$ K$^{-1}$).
- $D_a$: atmospheric vapor pressure deficit (Pa).
- $DM$: dry matter.
- $d$: number of days in the month.
- $d_1$, $d_2$: empirical descriptors of the response of $g_{sM}$ to $D_a$ (Pa) (Table 2).
- $E_c$: evaporation of water from the soil surface (mm).
- $E_t$: transpiration of water from the leaf canopy (mm).
- $E_{tot}$: annual water-use by vegetation (mm yr$^{-1}$).
- $G_s$: soil heat flux ($W$ m$^{-2}$).
- $g_a$: canopy aerodynamic conductance to water vapor flux ($m^2s^{-1}$).
- $g_{cut}$: cuticular conductance to water vapor flux ($mmol H_2O m^{-2}s^{-1}$).
- $g_t$: aerodynamic conductance to water vapor flux at the forest floor ($m^2s^{-1}$).
- $g_s$: canopy stomatal conductance to water vapor flux ($m^2s^{-1}$).
- $g_{sM}$: $g_s$ on a molar basis ($mmol H_2O m^{-2}s^{-1}$).
- $g_W$: total canopy conductance to water vapor flux ($m^2s^{-1}$).
- $H$: sensible heat flux ($W$ m$^{-2}$).
- $h$: hour of the day.
- $J$: interception of rainfall by the leaf canopy (mm).
- $J_{max}$: light-dependent rate of electron transport ($\mu$mol electrons m$^{-2}$ s$^{-1}$).
- $K_c$: Michaelis-Menten affinity of Rubisco for CO$_2$ (Pa).
- $K_o$: Michaelis-Menten affinity of Rubisco for O$_2$ (kPa).
- $k_b$: canopy extinction coefficient for beam PAR (m$^{-2}$ ground area m$^{-2}$ leaf area).
- $k_{bs}$: canopy extinction coefficient for beam and scattered PAR (m$^{-2}$ ground area m$^{-2}$ leaf area).
- $k_{ds}$: canopy extinction coefficient for diffuse and scattered PAR (m$^{-2}$ ground area m$^{-2}$ leaf area).
- $k_M$: the rate of decline in $M$ with cumulative leaf area index (Table 2).
- $L$: leaf area index ($m^2$ leaf area m$^{-2}$ ground area).
- $L_a$: actual canopy $L$ ($m^2$ leaf area m$^{-2}$ ground area).
- $L_c$: upward or downward flux of longwave radiation from the canopy ($W$ m$^{-2}$).
- $L_d$: downward flux of longwave radiation from the sky ($W$ m$^{-2}$).
- $L_e$: the canopy $L$ effective in absorbing radiation ($m^2$ leaf area m$^{-2}$ ground area).
- $L_s$: upward flux of longwave radiation from the soil ($W$ m$^{-2}$).
- $M$: leaf mass:area ratio (g DM m$^{-2}$).
- $M_0$: $M$ in the uppermost leaves of the canopy (g DM m$^{-2}$).
- $M_c$: value of $M$ for the whole leaf canopy (g DM m$^{-2}$).
- $M_L$: $M$ in leaves beneath a leaf area index of $L$ (g DM m$^{-2}$).
- $M_{min}$: minimum viable value of $M$ in shaded leaves at the bottom of the canopy (g DM m$^{-2}$) (Table 2).
- $m$: month of the year.
- $m_C$: molecular mass associated with each carbon atom in carbohydrates [CH$_2$O]$_3$ 30 (dimensionless).
- $N_a$: area-based leaf nitrogen content (g m$^{-2}$).
- $N_c$: NIR absorbed by the leaf canopy ($W$ m$^{-2}$).
- $N_{cr}$: coarse root nitrogen concentration (mg N g$^{-1}$ DM) (Table 2).
- $N_{cr}$: ephemeral root nitrogen concentration (mg N g$^{-1}$ DM) (Table 2).
- $N_l$: leaf nitrogen concentration (mg N g$^{-1}$ DM).
- $N_i$: nitrogen concentration in plant partition $i$ ($N_l, N_s, N_{cr}$ or $N_{cr}$) (mg N g$^{-1}$ DM).
- $N_i$: incident flux of NIR ($W$ m$^{-2}$).
- $N_p$: plant nitrogen demand (g N m$^{-2}$ ground area yr$^{-1}$).
- $N_s$: sapwood nitrogen concentration (mg N g$^{-1}$ DM) (Table 2).
- $N_{l}$: re-translocation of nitrogen from senescing leaves (g N m$^{-2}$ ground area yr$^{-1}$).
- $N_u$: root uptake of nitrogen from the soil (g N m$^{-2}$ ground area yr$^{-1}$).
- $NIR$: near infrared radiation.
- $O_l$: partial pressure of O$_2$ within the leaf (21 kPa).
- $P$: atmospheric pressure (Pa).
- $P_e$: PAR absorbed by the leaf canopy ($W$ m$^{-2}$).
- $P_i$: incident flux of PAR ($W$ m$^{-2}$).
- $P_{i}$: $P_{i}$ partitioned to plant part $i$ ($P_l, P_s$, or $P_e$) (g DM m$^{-2}$ yr$^{-1}$).
\[ P_1 \] net primary productivity (g DM m\(^{-2}\) yr\(^{-1}\)).
\[ P_n \] net primary productivity (g DM m\(^{-2}\) yr\(^{-1}\)).
\[ P_r \] partitioned to roots (g DM m\(^{-2}\) yr\(^{-1}\)).
\[ P_s \] partitioned to sapwood (g DM m\(^{-2}\) yr\(^{-1}\)).
\[ \rho \] precipitation (mm month\(^{-1}\)).
\[ Q \] absorption of photosynthetically active quanta (\(\mu\)mol quanta m\(^{-2}\) s\(^{-1}\)).
\[ Q_e \] for the whole canopy (\(\mu\)mol quanta m\(^{-2}\) ground area s\(^{-1}\)).
\[ Q_s \] for the sunlit population of canopy leaves (\(\mu\)mol quanta m\(^{-2}\) ground area s\(^{-1}\)).
\[ Q_{sh} \] for the shaded population of canopy leaves (\(\mu\)mol quanta m\(^{-2}\) ground area s\(^{-1}\)).
\[ R_a \] canopy respiration rate on a mass basis, excluding photosynthesis (\(\mu\)mol CO\(_2\) cm\(^{-2}\) s\(^{-1}\)).
\[ R_{M} \] canopy respiration rate on a mass basis, excluding photosynthesis (\(\mu\)mol CO\(_2\) g\(^{-1}\) s\(^{-1}\)).
\[ R_r \] root maintenance respiration rate (\(\mu\)mol CO\(_2\) m\(^{-2}\) ground area s\(^{-1}\)).
\[ R_s \] sapwood maintenance respiration rate (\(\mu\)mol CO\(_2\) m\(^{-2}\) ground area s\(^{-1}\)).
\[ r_Q \] sensitivity of respiration to \(Q\) (dimensionless).
\[ r_N \] sensitivity of root respiration to nitrogen (\(\mu\)mol CO\(_2\) g\(^{-1}\) N s\(^{-1}\)) (Table 2).
\[ r_T \] temperature sensitivity of respiration (dimensionless).
\[ r_v \] rate of sapwood respiration on a volume basis (\(\mu\)mol CO\(_2\) m\(^{-3}\) s\(^{-1}\)) (Table 2).
\[ s \] the rate of change in saturation vapor pressure with temperature (Pa K\(^{-1}\)).
\[ s_C \] soil carbon content (g C m\(^{-2}\) ground area).
\[ s_N \] soil nitrogen content (g N m\(^{-2}\) ground area).
\[ s_{min} \] minimum relative value of \(g_{AM}\) normally occurring under drought conditions in the field (dimensionless) (Table 2).
\[ s_f, s_2 \] empirical descriptors of the response of \(g_{AM}\) to \(w_d\) (dimensionless) (Table 2).
\[ T_a \] air temperature (K).
\[ T_c \] canopy temperature (K).
\[ V_{c,max} \] carboxylation capacity for Rubisco on an area basis (\(\mu\)mol CO\(_2\) m\(^{-2}\) s\(^{-1}\)).
\[ V_m \] carboxylation capacity for Rubisco on a mass basis (\(\mu\)mol CO\(_2\) g\(^{-1}\) s\(^{-1}\)).
\[ V_s \] for the sunlit population of canopy leaves (\(\mu\)mol CO\(_2\) m\(^{-2}\) s\(^{-1}\)).
\[ V_{sh} \] for the shaded population of canopy leaves (\(\mu\)mol CO\(_2\) m\(^{-2}\) s\(^{-1}\)).
\[ v_s \] sapwood volume (m\(^3\) m\(^{-2}\) ground area).
\[ W_r \] root biomass (g DM m\(^{-2}\)).
\[ W_a \] soil water availability between the field capacity and permanent wilting point (expressed as a dimensionless fraction).
\[ Y_G \] efficiency of dry matter production from fixed carbon (additional subscripts l, s, or r denote leaves, sapwood, or roots, respectively) (g DM g\(^{-1}\) glucose) (Table 2).
\[ Z_l \] leaf lifespan (months).
\[ Z_r \] root lifespan (yr).
\[ \alpha_n \] leaf NIR absorptance (dimensionless) (Table 2).
\[ \alpha_p \] leaf PAR absorptance (dimensionless) (Table 2).
\[ \alpha_s \] soil absorptance, 0.88 (dimensionless) [Campbell and Norman, 1998].
\[ \alpha_{sh} \] absorptance of shortwave radiation by tree trunks and branches, 0.80 (dimensionless) [Tamai et al., 1998; Wilson et al., 2000b].
\[ \beta \] ratio of actual to potential \(\lambda E_a\) (dimensionless).
\[ \chi \] fraction of the land surface covered by tree canopies (dimensionless).
\[ \Phi_a \] net radiation at the canopy surface (W m\(^{-2}\)).
\[ \Phi_s \] net radiation at the soil surface (W m\(^{-2}\)).
\[ \phi \] quantum efficiency of electron transport, 0.24, (mol electrons mol\(^{-1}\) quanta) [Harley et al., 1992].
\[ \gamma \] psychrometer constant (Pa K\(^{-1}\)).
\[ \varphi_t \] fraction of \(W_t\) comprising ephemeral roots (Table 2).
\[ \lambda E \] latent heat flux (W m\(^{-2}\)).
\[ \lambda E_a \] \(\lambda E\) attributable to the evaporation of water from the soil surface (W m\(^{-2}\)).
\[ \lambda E_d \] \(\lambda E\) attributable to the evaporation of rainfall wetting the canopy (W m\(^{-2}\)).
\[ \theta \] solar zenith angle (rad).
\[ \rho_a \] the density of dry air (1.204, kg m\(^{-3}\)).
\[ \rho_b \] canopy reflection coefficient for beam PAR, (dimensionless).
\[ \rho_d \] canopy reflection coefficient for diffuse PAR (dimensionless).
\[ \sigma_r \] age-related relative decline in \(V_{c,max}\) and \(R_d\) (dimensionless).
\[ \sigma_{min} \] minimum annual value of \(\sigma_r\) (dimensionless).
\[ \Omega \] foliage clumping index (dimensionless) (Table 2).

References


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