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# Parameterization and Sensitivity Analysis of the BIOME-BGC Terrestrial Ecosystem Model: Net Primary Production Controls

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**ABSTRACT:** Ecosystem simulation models use descriptive input parameters to establish the physiology, biochemistry, structure, and allocation patterns of vegetation functional types, or biomes. For single-stand simulations it is possible to measure required data, but as spatial resolution increases, so too does data unavailability. Generalized biome parameterizations are then required. Undocumented parameter selection and unknown model sensitivity to parameter variation for larger-resolution simulations are currently the major limitations to global and regional modeling. The authors present documented input parameters for a process-based ecosystem simulation model, BIOME-BGC, for major natural temperate biomes. Parameter groups include the following: turnover and mortality; allocation; carbon to nitrogen ratios (C:N); the percent of plant material in labile, cellulose, and lignin pools; leaf morphology; leaf conductance rates and limitations; canopy water interception and light extinction; and the percent of leaf nitrogen in Rubisco (ribulose biphosphate-1,5-carboxylase/oxygenase) (PLNR). Using climatic and site de-

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scription data from the Vegetation/Ecosystem Modeling and Analysis Project, the sensitivity of predicted annual net primary production (NPP) to variations in parameter level of  $\pm 20\%$  of the mean value was tested. For parameters exhibiting a strong control on NPP, a factorial analysis was conducted to test for interaction effects. All biomes were affected by variation in leaf and fine root C:N. Woody biomes were additionally strongly controlled by PLNR, maximum stomatal conductance, and specific leaf area while nonwoody biomes were sensitive to fire mortality and litter quality. None of the critical parameters demonstrated strong interaction effects. An alternative parameterization scheme is presented to better represent the spatial variability in several of these critical parameters. Patterns of general ecological function drawn from the sensitivity analysis are discussed.

**KEYWORDS:** Biogeochemical processes; Plant ecology; Land/atmosphere interactions

## 1. Introduction and background

Terrestrial net primary production (NPP,  $\text{g m}^{-2}$ ), equal to gross primary production minus autotrophic respiration, represents the carbon available for plant allocation to leaves, stems, roots, defensive compounds, and reproduction and is the basic measure of biological productivity. Tree growth, forage available for grazing, food production, fossil fuel production, and atmospheric  $\text{CO}_2$  levels are all strongly controlled by NPP. Accurate quantification of NPP at local to global scales is therefore central topic for carbon cycle researchers, foresters, land and resource managers, and politicians. For recent or current NPP estimates, satellite remote sensing can be used (e.g., Potter et al. 1993) but for research investigating pre-1970s time periods or future climate scenarios, simulation models are required.

Models have been used to simulate regional water and carbon cycles under current and historical climates (Nemani et al. 1993; Running 1994), soil carbon dynamics (Motovalli et al. 1994), effects of nitrogen saturation (Aber et al. 1997), and the location of global carbon sources and sinks (Houghton et al. 1998; Randerson et al. 1997). Models can also be used to develop basic theoretical understandings of ecosystem function that cannot be tested with field methods (Churkina and Running 1998; Schimel et al. 1996). Perhaps most importantly, models are used to address the political and management need for estimates of ecosystem responses to climate changes (Intergovernmental Panel on Climate Change 1995). In particular, as fossil fuel consumption exponentially increases atmospheric  $\text{CO}_2$  (Keeling 1994) there is a growing need to provide credible estimates of ecosystem storage or release of carbon (Hunt et al. 1996; Schimel et al. 2000). NPP is a common component of these modeling approaches.

Large-scale biogeochemical (BGC) modeling, the topic of this research, is a specific type of modeling that seeks to mechanistically represent ecosystem cycles of carbon, water, and nutrients at regional to global scales through an integrated consideration of biology and geochemistry. The simulated land surface is divided into grid cells described by vegetation type (land cover), slope, aspect, elevation, albedo, and soil depth and texture (e.g., from Zobler 1986) from which soil water

holding capacity and water release properties may be calculated (Clapp and Hornberger 1978). Nitrogen deposition, CO<sub>2</sub> concentration, and climate data (usually monthly or daily) describe the atmosphere. Mathematical equations representing an abstraction of reality are then used to simulate ecosystem cycles of carbon (assimilation and respiration), nitrogen (mineralization, immobilization, leaching, volatilization, and denitrification), and water (evaporation, transpiration, and runoff).

The theoretical basis for NPP predictions and other model processes is usually based on realistic laboratory or field research, yet this same model realism often translates to a seemingly endless proliferation of difficult to obtain driving inputs, or parameters. In some cases, parameters are measured for a particular study, but when left unconstrained by measurement, parameters can be used as tuning knobs capable of producing a wide range of outputs. We feel that for these reasons, parameter selection and documentation, not model theory, are the main factors currently limiting the accuracy and believability of global and regional model simulations. As Aber (Aber 1997) stated: “ALL of the parameters used in the model should be listed, and ALL values for those parameters given, along with the references to the sources of those parameters.” Aber also argued for complete descriptions of model structure and sensitivity. To address these and related concerns, our goals in this research are to

- provide an account of the source (or lack thereof) for parameters in BIOME-BGC, a commonly used terrestrial ecosystem process model, for major temperate biomes;
- assess the sensitivity of NPP to independent variation in every parameter;
- conduct a factorial sensitivity analysis of the most critical parameters;
- investigate patterns of ecosystem function revealed by the sensitivity analysis; and
- present a blueprint for an alternative parameterization scheme for critical parameters.

## **2. Materials and methods**

### **2.1 BIOME-BGC**

Using prescribed site conditions, meteorology, and parameter values, BIOME-BGC simulates daily fluxes and states of carbon, water, and nitrogen for coarsely defined biomes at areas ranging from 1 m<sup>2</sup> to the entire globe. Plant physiological processes respond to diurnal environmental variation (Geiger and Servaites 1994), but BIOME-BGC uses a daily time step in order to take advantage of widely available daily temperature and precipitation data from which daylight averages of short wave radiation, vapor pressure deficit, and temperature are estimated (Thornton et al. 1997; Thornton and Running 1999). Nonlinear diurnal photosynthetic responses to radiation levels will not be captured by the use of daylight average radiation, but models initially designed to operate at daily timescales may still be used to accurately represent short-term variation in carbon fluxes (Kimball et al. 1997b).

BIOME-BGC simulates the development of soil and plant carbon and nitrogen pools; no input of soil carbon information or leaf area index (LAI, m<sup>2</sup> leaf area per m<sup>2</sup> ground area) is required. LAI controls canopy radiation absorption, water interception, photosynthesis, and litter inputs to detrital pools and is thus central to BIOME-BGC. Model structure is discussed by Thornton (Thornton 1998) and is available online ([www.forestry.umd.edu/ntsg](http://www.forestry.umd.edu/ntsg)), and will not be presented here. Briefly, though, NPP is based on gross primary production simulated with the Farquhar photosynthesis model (Farquhar et al. 1980) minus maintenance respiration [calculated as a function of tissue nitrogen concentration (Ryan 1991)] and growth respiration (a constant fraction of gross primary production). Theory and applications of BIOME-BGC and its predecessor, FOREST-BGC, are widely available (e.g., Hunt et al. 1996; Kimball et al. 1997b; Kimball et al. 1997c; Running 1994; Running and Coughlan 1988; Running and Gower 1991; Running and Hunt 1993; Running and Nemani 1991; White et al. 1999).

In BIOME-BGC, 34 parameters within several main categories are used to distinguish separate biomes. 1) Turnover and mortality parameters are used to describe the portion of the plant pools that are either replaced each year or removed through fire or plant death. 2) The allocation of photosynthetically accumulated carbon to leaf, stem, and root pools is controlled by a series of allometric parameters. 3) Carbon to nitrogen ratios define nutrient requirements for new growth, plant respiration rates, photosynthetic capacity, and litter quality. 4) The percentage of lignin, cellulose, and labile material in fine roots, leaves, and dead wood controls litter recalcitrance and influences decomposition rates. 5) Three morphological parameters control the distribution of LAI at the leaf and canopy level. 6) Several ecophysiological parameters are used to control rates of and limitations to leaf conductance. 7) Single parameters are used to control water interception, canopy radiation absorption, and the rate of carbon assimilation. Conceptually, the parameter groups describe biomes by rejecting excessive detail and unobtainable parameters while maintaining broadly significant vegetation descriptions.

## 2.2 Parameterization

For each parameter we conducted a literature search for each biome and calculated mean and standard deviation. There were two choices when assigning values: use the mean for each biome or conduct multiple comparison tests to group biome values together into statistically similar groups. Natural variability within biomes and, in some cases, limited sample sizes led the statistical approach to produce a homogeneous parameterization wherein biomes were remarkably indistinguishable. Since the ecological relevance of biome differences is well recognized (T. M. Smith et al. 1997) we chose the first option and did not test for statistically significant differences.

Data were usually available for evergreen needle leaf forest (ENF) and deciduous broadleaf forest (DBF), but in the grass literature, C<sub>4</sub> data were rare and many authors reported “grasslands” without C<sub>3</sub>/C<sub>4</sub> discrimination. We therefore parameterized a single grass biome. The C<sub>4</sub> grass (C4G) is simulated with simple mechanisms to concentrate CO<sub>2</sub> levels and to increase quantum yield efficiency.

While some parameters were adequately treated for deciduous needle leaf forest (DNF), data for allocation parameters, the percent labile, cellulose, and lignin content in fine roots, litter, and dead wood, and leaf water stress parameters were lacking. With one exception related to photosynthesis, we applied the ENF values to DNF. Since data for shrubs were often sparse, defining multiple shrub categories, while perhaps ecologically appealing, was impractical. When shrub data were unavailable, we again generally assumed ENF values (see appendix A for exceptions).

## 2.3 Sensitivity analysis

### 2.3.1 Inputs

We used BIOME-BGC and the  $0.5^\circ \times 0.5^\circ$  continental U.S. Vegetation/Ecosystem Modeling and Analysis Project (VEMAP) dataset (Pan et al. 1998; VEMAP 1995) to simulate NPP. VEMAP provided daily meteorology (T. G. F. Kittel et al. 2000, manuscripts in preparation; Kittel et al. 1997) for both preindustrial (1795–1894) and industrial (1895–1993) periods, soil texture and depth (Kern 1994; Kern 1995), and land cover (Küchler 1964; Küchler 1975). We reclassified the land cover into six classes: ENF, shrub, DNF [not represented at 0.5 resolution, distribution in Gower and Richards (Gower and Richards 1990) used to identify known areas], DBF, C<sub>3</sub> grass (C3G), and C4G. To estimate VEMAP preindustrial nitrogen deposition, we first calculated a linear precipitation to deposition regression equation from a global 14-yr daily gridded meteorology dataset (Piper 1995) and total global preindustrial nitrogen deposition estimated from data in Holland et al. (Holland et al. 1997). We then applied the same relationship to the VEMAP preindustrial precipitation levels. We estimated industrial nitrogen deposition with  $5^\circ \times 5^\circ$  MOGUNTIA (Dentener and Crutzen 1994; Zimmermann et al. 1989) predictions scaled to the 0.5 VEMAP resolution.

### 2.3.2 Process

Any given simulation followed a two-step procedure. First, using preindustrial meteorology, CO<sub>2</sub> levels, and nitrogen deposition, soil carbon and nitrogen pools were initialized with BIOME-BGC simulations that terminated when equilibrium levels of net ecosystem carbon exchange were attained, typically 500–4000 yr. Second, the 1895–1993 period was simulated with increasing levels of CO<sub>2</sub> [(VEMAP 1995), from ice core and atmospheric measurements]. Nitrogen deposition was increased from preindustrial to industrial (1990) levels at the same rate as CO<sub>2</sub> increases.

### 2.3.3 Independent variation sensitivity analysis

We executed the sensitivity analysis with independent parameter variation as follows. We randomly selected 10 pixels for each of the six biomes (appendix B) and tested the effect of varying each parameter independently of other parameters by plus or minus a constant percent value. Ideally we would have varied the parameters within their measured range of variability, but because some parameters were based on a single value or used values from a different biome, such

an approach was impracticable. Instead we calculated one-tailed 95% confidence intervals and then calculated the average confidence interval (expressed as a percent of the mean value; only parameters based on at least two individual values were included). We varied parameters by the mean confidence interval (to one significant digit). We then arranged the parameters by the significance of their impact on NPP and identified the parameters most dominating BIOME-BGC predictions.

### **2.3.4 Factorial sensitivity analysis**

For these limited parameters, we then adopted the suggestion of Henderson-Sellers and Henderson-Sellers (Henderson-Sellers and Henderson-Sellers 1996) and conducted a fractional factorial analysis [half-fraction approach in chapter 12 of Box et al. (Box et al. 1978)] to calculate main and interaction effects for two representative biomes. A factorial approach detects interacting effects of parameter variation, information that is impossible to obtain from varying parameters independently. In this case, the critical parameters were well documented and we used the measured range of parameter variability in the analysis. The range of variability used in factorial analysis is subjective and we initially used the standard deviation as the measure of variability. However, in the case where all critical parameters were set at levels expected to produce decreases in NPP, BIOME-BGC did not simulate biome development (i.e., the simulation “crashed”). We therefore used the standard error as the measure of variability. We calculated main and interaction effects for each of the 10 pixels per biome and then calculated the mean and confidence interval of the effects.

## **2.4 Ecosystem synthesis and alternative parameterization**

We then analyzed the results of the parameterization and sensitivity analysis for patterns of consistent biome and ecosystem function. Finally, we explored schemes to predict the spatial variability of critical parameters.

## **3. Results and discussion**

### **3.1 Parameterization**

Table 1 shows mean values for each parameter. Full parameter descriptions and a discussion of their role in BIOME-BGC, statistical information, species names, and citations are included in appendix A.

### **3.2 Sensitivity analysis**

#### **3.2.1 Independent variation sensitivity analysis**

The mean confidence interval (expressed as percent of parameter mean) was 20%. Results from the sensitivity analysis in which parameters were independently varied  $\pm 20\%$  show two key findings (Table 2): 1) only a small number of parameters consistently produced statistically significant differences in simulated



NPP and 2) the groups of important parameters were different between woody and nonwoody biomes.

Parameter  $C:N_{\text{leaf}}$  is the only one that exerted a significant control on NPP for all biomes (Table 2). For the woody biomes (ENF, shrub, DNF, and DBF), increasing  $C:N_{\text{leaf}}$  decreased NPP, while in C3G and C4G, increased  $C:N_{\text{leaf}}$  had the opposite effect, increasing NPP. Thus, for woody biomes an increased leaf nitrogen investment and higher respiration cost was more than offset by increases in photosynthesis while in nonwoody biomes the opposite was true. PLNR (which strongly controls maximum rate of carboxylation), which had the largest effect for woody biomes but no significant effect in C3G and C4G (Table 2), is the main reason for this effect. Compared to the grasses, the woody biomes had low PLNR (Table 1); slightly increasing  $C:N_{\text{leaf}}$  reduced the amount of nitrogen available for investment in ribulose biphosphate-1,5-carboxylase/oxygenase (Rubisco). In these biomes, the amount of Rubisco at mean  $C:N_{\text{leaf}}$  already limited the maximum rate of carboxylation and increasing  $C:N_{\text{leaf}}$  created an even more severe photosynthetic limitation. Conversely, in the grass biomes, even at the mean minus 20% PLNR, Rubisco was still abundant and did not limit photosynthesis. By increasing  $C:N_{\text{leaf}}$ , grasses did not reduce photosynthetic capacity but they did reduce the cost of creating and maintaining leaves; a larger canopy and higher NPP were simulated. Increased leaf nitrogen investment in grasses simply created a nitrogen cost without increasing photosynthetic capacity.

In all biomes except DNF, higher  $C:N_{\text{fr}}$  increased NPP by making more nitrogen available for investment in leaves. Unlike for  $C:N_{\text{leaf}}$ , increases in  $C:N_{\text{fr}}$  do not have a negative physiological consequence for any biome and purely increase the pool of nitrogen available for investment in beneficial plant pools such as Rubisco. Beyond these two C:N parameters, the significant parameters diverge for woody and grass biomes.

In woody biomes, three more parameters consistently impacted simulated NPP. First, increased new fine root carbon to new leaf carbon allocation (FRC:LC) diverted carbon from leaves into fine roots, but because BIOME-BGC does not mechanistically simulate root processes, it had no effect of increasing the efficiency of root nitrogen uptake. NPP therefore declined when FRC:LC was increased. Second, increased specific leaf area (SLA) resulted in higher LAI ( $\text{LAI} = \text{SLA} \times \text{leaf carbon}$ ) without altering photosynthetic capacity, increasing water stress and reducing NPP. Third, increases in  $g_{\text{smax}}$  reduced NPP by increasing water stress. The increases in potential leaf  $\text{CO}_2$  uptake caused by higher  $g_{\text{smax}}$  were negated by increased depletion of soil water early in the growing season leading to stomatal down regulation of conductance later in the growing season. Parameters with a more limited effect included leaf and fine root turnover (LFRT, increased ENF NPP),  $\text{LAI}_{\text{all:proj}}$  (decreased ENF NPP),  $W_{\text{int}}$  (decreased ENF NPP), and  $k$  (decreased DBF NPP). In general, parameters decreasing LAI [high FRC:LC,  $g_{\text{smax}}$ ,  $\text{LAI}_{\text{all:proj}}$ , and  $W_{\text{int}}$  (LAI data not shown)] decreased NPP, but LAI increases independent of increases in leaf nutrition (higher SLA) also decreased NPP.

In grass biomes, fire mortality (FM) and parameters relating to litter quality were far more important. Increasing FM, which increases nitrogen volatilization and reduces available mineral nitrogen, produced the largest NPP sensitivity for

C3G and C4G but no discernable response for any woody biome. Increasing litter quality, as seen by significant effects from high levels of  $FR_{cel}$ ,  $FR_{lab}$ ,  $L_{cel}$ , and  $L_{lab}$ , increased NPP, while reducing litter quality (high  $FR_{lig}$ ) reduced NPP. Higher quality litter and fine roots decompose more rapidly than low quality material and increase the amount of nitrogen available for plant uptake.

### 3.2.2 Factorial sensitivity analysis

Because of similar behavior within woody and nonwoody biomes, we selected only two biomes for the half-fraction factorial analysis: ENF for woody and C3G for nonwoody. For ENF we selected  $C:N_{leaf}$ ,  $g_{smax}$ , PLNR, SLA, and  $C:N_{fr}$ . The variable FRC:LC was also important in the independent parameter analysis, but due to uncertainties in parameter variance and methodological difficulties inherent in obtaining the parameter (appendix A), we excluded FRC:LC from the design. For C3G, we used  $C:N_{leaf}$ , FM,  $FR_{cel}$ ,  $L_{cel}$ , and  $C:N_{fr}$ .

In the half-fraction factorial design of  $n$  parameters,  $2^{n-1}$  simulations, or half the number of a full factorial design, are used (Box et al. 1978). Simulation time is halved with extremely small differences from the full factorial. Table 3 shows the design of the half-fraction [see Box et al. (Box et al. 1978) for details on constructing the table of contrast coefficients and calculating main and interaction terms].

Main effects are conceptually similar to the results from the independent parameter variation analysis but in this case were produced by runs with parameters set plus or minus their measured range of variability. Table 4 shows the main effect caused by increasing the parameter from the mean minus the standard error to the mean plus the standard error. All five main effects were statistically significant for both biomes. Consistent with results from the independent parameter analysis (Table 2), ENF was most affected by variation in PLNR while in C3G, FM had the largest effect. All main effects were at least 5.9 times larger than their standard errors.

Interaction effects (Table 5) show the difference between what would be expected by adding up the two main effects and what was actually observed from the interaction. For example, the ENF  $C:N_{leaf} \times PLNR$  interaction produced a  $2.9 \text{ g m}^{-2}$  larger effect than would be expected from the sum of the  $C:N_{leaf}$  and PLNR main effects, indicating that the negative effects of increased  $C:N_{leaf}$  were lessened by interacting increases in PLNR. The other two significant interaction effects were  $g_{smax} \times C:N_{fr}$  and  $SLA \times C:N_{fr}$ , both of which indicated that increased water stress caused by high  $g_{smax}$  or SLA dampened the increase in NPP caused by higher  $C:N_{fr}$ .

Interaction effects were often an order of magnitude less than main effects and the largest interaction term was 4.8 (4.7) times smaller than the smallest main effect in ENF (C3G). In C3G, no interaction term was significant and in ENF, only 3 out of 10 interactions were significant. To summarize, results from the factorial analysis presented in Tables 3–5 show that main effects are extremely dominant over interaction effects and that changes in simulated NPP can be approximated from the magnitude of the main effects in Table 4.



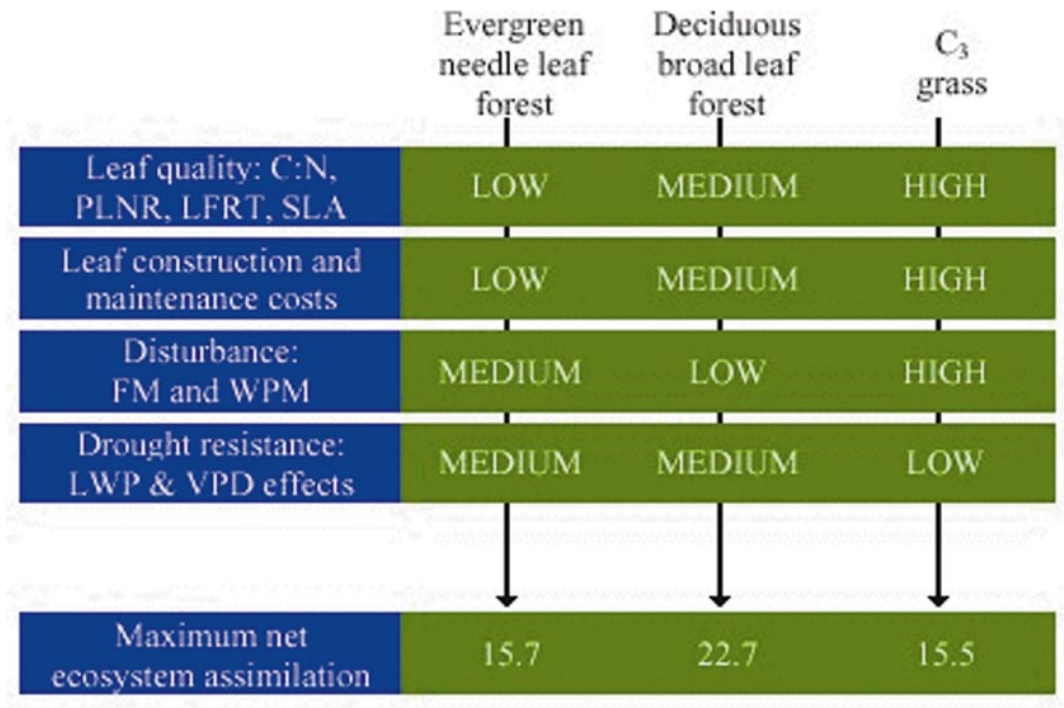


Figure 1. Conceptual chart of biome-level parameter groups and resulting maximum net ecosystem assimilation rates. Parameter categories (left boxes) are as follows. 1) Leaf quality is a function of C:N<sub>leaf</sub>, the percent of leaf nitrogen in Rubisco (PLNR), LFRT (leaf and fine root turnover), and specific leaf area (SLA). Low C:N<sub>leaf</sub>, high PLNR, high LFRT, and high SLA create high photosynthetic capacity foliage. 2) Leaf costs represent the carbon and nitrogen costs to construct and maintain foliage. 3) Disturbance includes fire mortality (FM) and whole plant mortality (WPM). 4) Drought resistance represents plant ability to regulate stomatal conductance under vapor pressure deficit (VPD) and leaf water potential (LWP) stresses. Bottom panels show the average maximum net ecosystem assimilation rates ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) for each biome (Buchmann and Schulze 1999).

### 3.3 Parameter associations and NPP limitations

In a global survey of multiple vegetation types, Reich et al. (Reich et al. 1997; Reich et al. 1999) found strong linkages between SLA, leaf longevity, and leaf nitrogen concentration. In summary, high rates of net carbon assimilation at the leaf level = high SLA = short leaf longevity = high leaf nitrogen concentration. Conceptually, the results showed that plants exist along a continuum from short-lived, high productivity to long-lived, less productive foliage. Here, even though we considered biome means and not continuous vegetation gradients, we found similar patterns in the three best-referenced biomes (Figure 1).

Yet the parameter association identified by Reich et al. (Reich et al. 1997; Reich et al. 1999) as increasing instantaneous rates of assimilation do not necessarily result in increased assimilation at the ecosystem level (Figure 1). In all biomes, increased SLA increased LAI (data not shown) yet decreased NPP (Table 2) through a feedback from increased water stress. If NPP were limited by canopy assimilation capacity and not nitrogen availability (photosynthetic limitation), increasing leaf nitrogen would always increase NPP. For the woody biomes, this was true: increasing PLNR and reducing  $C:N_{\text{leaf}}$  increased NPP (Tables 2 and 4). For grasses, increased PLNR had little effect on NPP. Increasing grass  $C:N_{\text{leaf}}$ , because of high grass PLNR and reductions in maintenance respiration calculated as a function of tissue nitrogen (Ryan 1991), increased NPP. Retranslocation was also lowest in grass (appendix A), suggesting that high photosynthetic investment may reduce the ability to recover nitrogen, further enhancing growth limitations. Thus, grasses appear to be limited by their foliage nutrition, both in terms of construction nitrogen required and respiration costs.

Field research appears to support these concepts. In their global survey of average maximum net canopy assimilation rates ( $A_{\text{max}}$ , total canopy, not per LAI), Buchmann and Schulze (Buchmann and Schulze 1999) found that the ordinal relationship among biomes was DBF > grass ( $C_3$ ) ~ ENF. We speculate that the following general patterns, as illustrated in Figure 1, govern these results. In spite of optimal leaf nutrition, grass nitrogen limitations (to construct and maintain leaves), limited resistance to drought stresses, and high disturbance caused the low grass LAI found in Buchmann and Schulze (Buchmann and Schulze 1999). Thus a small grass canopy coupled with high photosynthetic capacity yields  $A_{\text{max}}$  values comparable to a large canopy of poor quality foliage in ENF. Longer growing seasons also compensate ENF for low quality foliage. With moderate controls on stomatal responses to water availability and moderate leaf nutrition and costs (Figure 1), DBF attained high LAI and the highest  $A_{\text{max}}$  of the three biomes (Buchmann and Schulze 1999).

### 3.4 Reduction in parameter uncertainty

While we have presented mean values, parameters should in reality vary spatially. For example, leaf longevity varies from about 2 yr to over 10 yr within the ENF (Figure 2, from appendix A). Cohesive patterns, such as decreasing leaf longevity at lower latitudes (Reich et al. 1995b), suggest the potential to spatially and realistically vary parameter levels. Not doing so may produce the correct spatially averaged NPP, but at any one location, over- or underestimation is likely. As a first attempt to reduce some of this uncertainty, we developed an approach to predict the spatial variability of  $C:N_{\text{leaf}}$ , SLA, LFRT, and PLNR.

We used published equations (Yin 1993) to predict the spatial variation of ENF and DBF  $C:N_{\text{leaf}}$  based on climatic variation (climate from the VEMAP dataset). We then predicted SLA and LFRT (leaf longevity) with the equations relating  $C:N_{\text{leaf}}$ , SLA, and leaf longevity developed by Reich et al. (Reich et al. 1997) and calculated PLNR based on the spatial variation of SLA and  $C:N_{\text{leaf}}$  (see appendix A for PLNR equation).

Mean values between the spatial method presented here and the data pre-

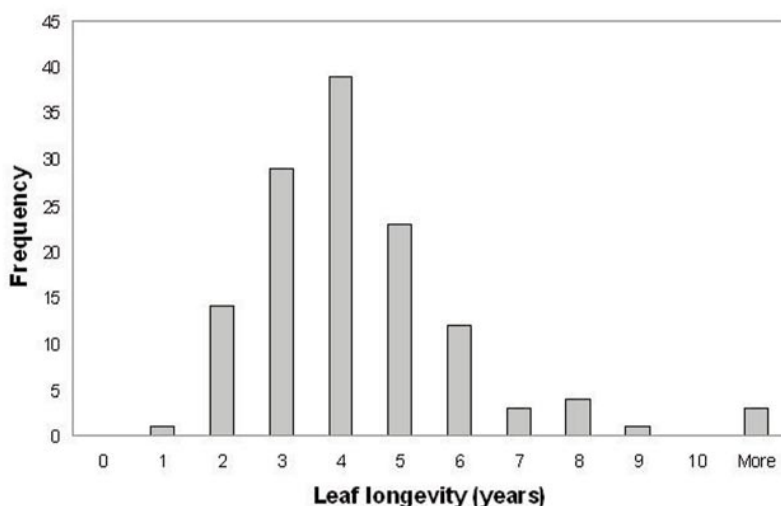


Figure 2. Frequency histogram of ENF leaf longevity. Data from appendix A.

sented above (Table 1) were generally similar for the ENF, but not for the DBF (Table 6). For ENF, mean  $C:N_{\text{leaf}}$ , SLA, leaf life span, and PLNR were all slightly higher in the spatial prediction (Figure 3) than in the single value per biome approach. Spatial patterns in Figure 3 were due entirely to initial  $C:N_{\text{leaf}}$ , which peaked in warm and cold climates (Minnesota and the far South) and reached a minimum in moderate climates. Large sections of the country were at approximately the same value for all four parameters. While the spatial prediction method produced mean values roughly comparable to the single value per biome approach, spatial patterns were troubling. For example, the methods in Yin (Yin 1993) predicted low nitrogen concentration in warm climates that in turn produced high leaf longevity in the south (Figure 3). Yet southern pine forests are known to have short leaf longevity (Reich et al. 1995b).

Mean DBF values showed significant differences between the two methodologies. In the spatial prediction (Figure 4),  $C:N_{\text{leaf}}$  was much higher than in the single value per biome approach. Consequently, the mean leaf life span was 13 months, more than twice as long as the leaf longevity predicted by the phenology subroutine (White et al. 1997) used in BIOME-BGC (Table 6). DBF SLA and PLNR were also low in the spatial prediction (Figure 4 and Table 6).

The prediction of very low SLA and numerous leaf life spans greater than 2 yr in the DBF and incorrect patterns of leaf longevity in the ENF are not acceptable results. We suspect that the range of climates used in Yin (Yin 1993) may not have been representative of the entire climatic range of the biome, thus leading to high  $C:N_{\text{leaf}}$  predictions in inappropriate areas. Note that in the north-eastern United States, where many of the studies in Yin (Yin 1993) were concentrated, DBF leaf life spans,  $C:N_{\text{leaf}}$ , and SLA were in a more normal range. These patterns illustrate both the exciting potentials of this methodology and its potential pitfalls. We believe that while this approach is conceptually superior to

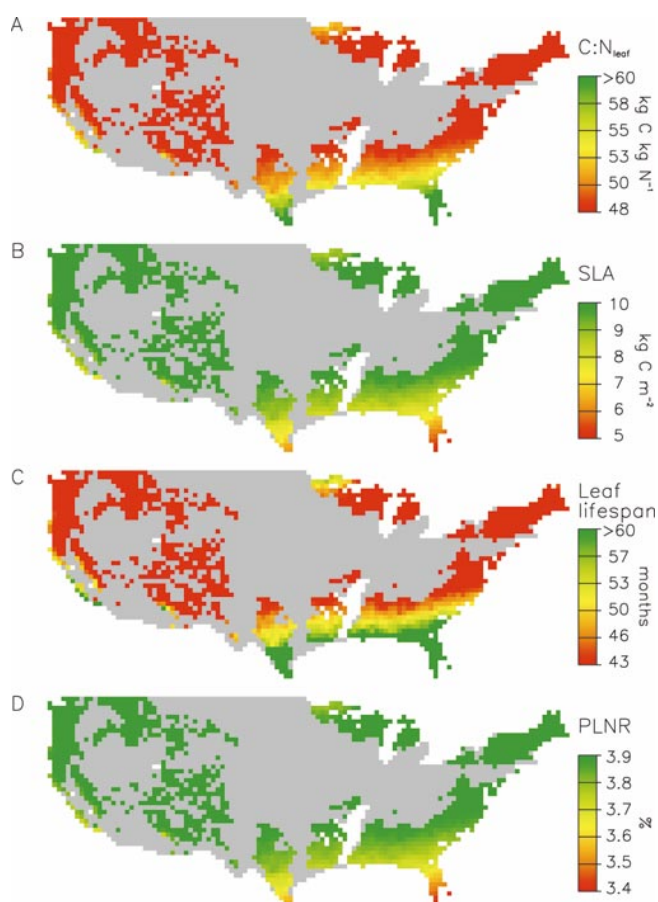


Figure 3. ENF parameter variation in the continental United States: (a)  $C:N_{leaf}$  ( $kg\ C\ kg\ N^{-1}$ ), (b) specific leaf area (SLA,  $kg\ C\ m^{-2}$ ), (c) leaf life span (months), and (d) the percent of leaf nitrogen in Rubisco (PLNR, dimensionless). Gray areas do not contain ENF in the VEMAP dataset.

using single values per biome, its adoption with the existing equations is premature. Future work should focus on predicting a more global distribution of  $C:N_{leaf}$  (appendix A; Reich et al. 1997; Reich et al. 1999) from site climate. Most studies do not publish climatic data, but with a global network of meteorological stations (Piper 1995) and a microclimate simulator (Glassy and Running 1994; Kimball et al. 1997a; Thornton and Running 1999), it is possible to estimate climate for any site.

The remaining critical parameters are more problematic. The parameter  $C:N_{fr}$  appears to follow consistent patterns with climate (Yin and Perry 1991), again suggesting the possibility of using site climate to predict  $C:N$ . However,  $C:N_{fr}$  calculation also relies on root diameter data, which are not currently available at large scales. We suggest that FRC:LC will be best obtained by calculation, not measurement. Given that the majority of other parameters are 1) better con-

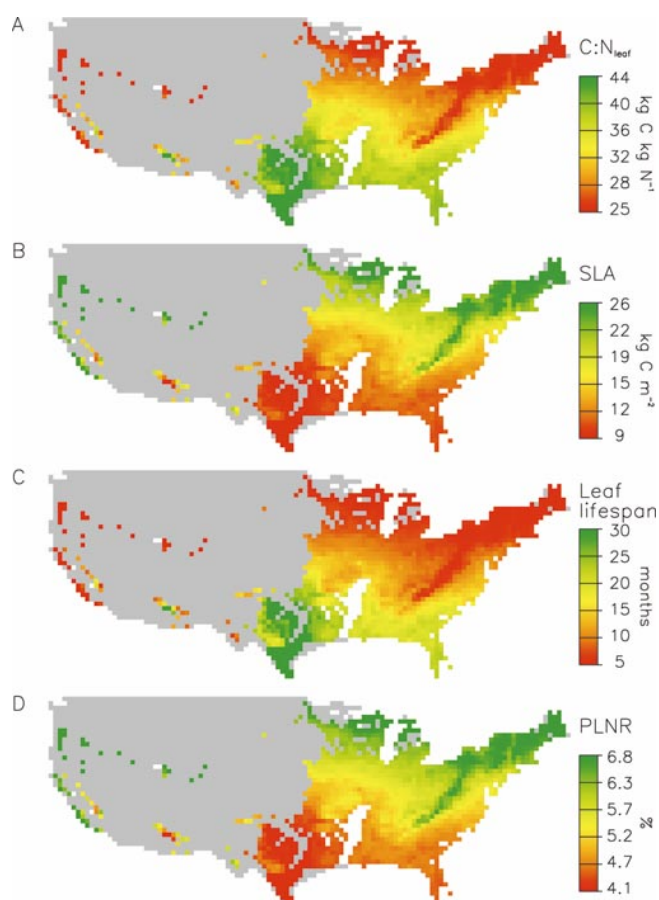


Figure 4. DBF parameter variation in the continental United States. Panels as in Figure 3. Gray areas do not contain DBF in the VEMAP dataset.

strained, 2) exert minor control over NPP, 3) could be fairly easily measured for a given site ( $C:N_{fr}$ ), or 4) could be resolved with the preceding scheme, it may be possible to solve for FRC:LC with an inverse method based on known values of total ecosystem exchange from eddy covariance methods (Baldocchi et al. 1996; Goulden et al. 1996). Currently, eddy covariance techniques are not adequate for this approach, but future improvements may make it possible. Reduction in FM uncertainty will require the development of a spatially variable global fire mortality dataset.

### 3.5 Suspicious results

While most of the results and interpretations presented above are fairly straightforward and follow logically from physiological and physiographic concepts, some of the results and parameterizations may be artifacts of model design or field data.



Increased  $C:N_{fr}$ , for example, reduces root nitrogen requirements and diverts nitrogen to increased photosynthetic capacity (higher NPP for most biomes; Table 2). Similarly, high FRC:LC diverts carbon to fine roots and away from LAI. Nitrogen and carbon are in essence allocated to the roots without any assimilation benefit from increased investment. In a purely mathematical sense, plants without roots will produce the highest NPP. However, it is well known that the vast majority of flowering plants maintain an active root system requiring carbon and nitrogen and we therefore include these costs in the model design. Adding the model complexity required to accurately model root density and distribution, ion gradients, mycorrhizal associations, etc. is not practical for large-scale ecological models, but should be considered for stand-specific efforts.

Reducing  $g_{smax}$  from  $0.006 \text{ m s}^{-1}$  increased NPP for every biome except C4G (Table 2), indicating that most biomes have nonoptimal  $g_{smax}$ . Nonoptimal levels for other parameters are usually somehow offset (i.e., poor leaf nutrition in ENF produces low respiration rates). For  $g_{smax}$ , it is not clear what compensates for the high water loss. While  $0.006 \text{ m s}^{-1}$  may represent the maximum possible  $g_{smax}$  under nonlimiting environmental conditions, average growing season  $g_{smax}$  may be more appropriate for ecosystem modeling. It is also possible that  $g_{smax}$  should also be reduced in the shaded canopy portion (Beadle et al. 1985; Kozlowski and Pallardy 1997; Oberbauer et al. 1987). Based on data showing  $g_{smax}$  reductions with leaf age (Field and Mooney 1983; Igboanugo 1996; Leverenz et al. 1982), it may further be realistic to reduce  $g_{smax}$  as a function of LFRT. Finally, if more data were available, it is possible that  $g_{smax}$  would vary statistically between biomes. Future research should focus on establishing the most appropriate  $g_{smax}$  values for ecosystem modeling approaches.

## 4. Conclusions and suggestions

For the first time in the history of BIOME-BGC and its predecessor, FOREST-BGC (Running and Coughlan 1988; Running and Gower 1991), we have produced a complete documentation of all model parameters and a comprehensive model sensitivity analysis for major natural temperate biomes. Major conclusions from the parameterization and sensitivity analysis include the following.

- Greatest NPP increases were created by 1) increasing leaf nitrogen content and nitrogen investment in Rubisco in woody biomes and by 2) reducing leaf nitrogen content and increasing nitrogen availability in nonwoody biomes.
- This suggests that productivity is photosynthetically limited for woody biomes and nitrogen limited for nonwoody biomes.
- Parameters varied logically such that biomes could not simultaneously have high productivity foliage, long leaf life span, low exposure to drought stresses, and low fire and mortality fluxes. Biomes tend to exist on a continuum from high quality foliage with a short and risky life span to low quality foliage with a long life and lower risk of fire and mortality.
- This research clearly shows why simplified NPP modeling approaches (Aber et al. 1996; Coops 1999) work well; for coarse time resolution

growth simulations, a very limited number of critical physiological variables are responsible for most output variation.

Simulations in other climates may produce a different list of critical parameters. We speculate that higher precipitation in the wet Tropics may eliminate SLA and  $g_{\text{max}}$  from the list and add controls on the absorption of radiation, such as the light extinction coefficient. The sensitivity analysis should therefore be expanded to include a more globally representative climatic distribution.

Exploration of more appropriate  $g_{\text{max}}$  values for modeling research and the implementation of mechanisms to regulate the efficiency of mineral nitrogen uptake as a function of root carbon and nitrogen investment should be future priorities. However, we believe that accurate predictions of the spatial distribution of several key parameters would produce the greatest reduction in the uncertainty of large-scale NPP simulations. We presented a blueprint for such an approach, but results were inconclusive. Further research on this topic is a critical priority.

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## Appendix A: Individual Parameter Values

Values presented here were converted from their original units to BIOME-BGC units. We assumed that carbon was 50% of dry weight. For parameters based on multiple literature values, we include summary statistics (mean, standard deviation, number of values) and individual citations. In cases where data were unavailable for DNF and shrub biomes, we used ENF values (exceptions noted below).

### A.1 Turnover and mortality parameters

Turnover refers to the percent of the carbon pool replaced each year (flux/mass) and is the inverse of the mean residence time (mass/flux). Mortality refers to the fraction of the carbon pool removed by plant death, either through whole plant mortality or fire mortality. Turnover and mortality parameters, with one exception, are relatively poorly documented parameters in BIOME-BGC and should be priorities for future work.

#### A.1.1 Leaf and fine root turnover

For all deciduous biomes, LFRT ( $1 \text{ yr}^{-1}$ ) is set to 1.0, indicating that the entire leaf and fine root carbon pools are turned over every year. The rationale for linking leaf and fine root turnover is presented in Thornton (Thornton 1998). ENF LFRT data are compiled from extensive foliage production and biomass data and shows mean leaf longevity of 3.8 yr. Values presented here are leaf turnover values. Original data were in leaf longevity. The mean value used in the parameterization is calculated from the inverse of the mean leaf longevity. A different

(and larger) value of leaf and fine root turnover is obtained by taking the mean of the values presented below.

ENF	Mean = 0.26, std dev = 0.15, $n = 129$	
<i>Abies amabilis</i>	0.093	(Gholz et al. 1976; Grier and Milne 1981; Grier et al. 1981)
<i>Abies amabilis</i>	0.047	(Gholz et al. 1976; Grier and Milne 1981; Grier et al. 1981)
<i>Abies balsamea</i>	0.270	(Baskerville 1965; Baskerville 1966)
<i>Abies balsamea</i>	0.270	(Baskerville 1965; Baskerville 1966)
<i>Abies balsamea</i>	0.263	(Baskerville 1965; Baskerville 1966)
<i>Abies balsamea</i>	0.270	(Baskerville 1965; Baskerville 1966)
<i>Abies balsamea</i>	0.270	(Baskerville 1965; Baskerville 1966)
<i>Abies balsamea</i>	0.278	(Baskerville 1965; Baskerville 1966)
<i>Abies concolor</i>	0.244	(Whittaker and Niering 1968; Whittaker and Niering 1975)
<i>Abies lasiocarpa</i>	0.227	(Whittaker and Niering 1968; Whittaker and Niering 1975)
<i>Abies procera</i>	0.182	(Fujimori et al. 1976)
<i>Abies sachalinensis</i>	0.233	(Satoo 1973)
<i>Abies veitchii</i>	0.294	(Tadaki et al. 1967)
<i>Abies veitchii</i>	0.208	(Tadaki et al. 1967)
<i>Abies veitchii</i>	0.192	(Tadaki et al. 1967)
<i>Abies veitchii</i>	0.196	(Tadaki et al. 1967)
<i>Abies veitchii</i>	0.345	(Tadaki et al. 1967)
<i>Abies veitchii</i>	0.185	(Tadaki et al. 1967)
<i>Abies veitchii</i>	0.213	(Tadaki et al. 1967)
<i>Abies veitchii</i>	0.313	(Tadaki et al. 1967)
<i>Abies veitchii</i>	0.233	(Tadaki et al. 1967)
<i>Abies veitchii</i>	0.286	(Kimura 1963; Kimura 1969; Kimura et al. 1968)
<i>Abies veitchii</i>	0.161	(Kimura 1963; Kimura 1969; Kimura et al. 1968)
<i>Abies veitchii</i>	0.175	(Kimura 1963; Kimura 1969; Kimura et al. 1968)
<i>Abies veitchii</i>	0.161	(Kimura 1963; Kimura 1969; Kimura et al. 1968)
<i>Abies veitchii</i>	0.139	(Kimura 1963; Kimura 1969; Kimura et al. 1968)
<i>Abies veitchii</i>	0.204	(Kimura 1963; Kimura 1969; Kimura et al. 1968)
<i>Abies veitchii</i>	0.185	(Kimura 1963; Kimura 1969; Kimura et al. 1968)
<i>Picea abies</i>	0.141	(Duvigneaud and Kestemont 1977; Kestemont 1975)
<i>Picea abies</i>	0.189	(Droste zu Hülshoff 1970; Ellenberg 1981a)
<i>Picea abies</i>	0.244	(Droste zu Hülshoff 1970; Ellenberg 1981a)
<i>Picea abies</i>	0.400	(Droste zu Hülshoff 1970; Ellenberg 1981a)
<i>Picea abies</i>	0.182	(Satoo 1971)
<i>Picea abies</i>	0.313	(Satoo 1971)
<i>Picea abies</i>	0.323	(Satoo 1971)
<i>Picea abies</i>	0.130	(Satoo 1971)
<i>Picea abies</i>	0.189	(Satoo 1971; Yoshimura 1967)
<i>Picea abies</i>	0.182	(Nihlgard 1972; Nihlgard and Lindgren 1977; Nihlgard and Lindgren 1981)
<i>Picea rubens</i>	0.088	(Gordon 1981)
<i>Picea rubens</i>	0.169	(Gordon 1981)
<i>Picea rubens</i>	0.123	(Gordon 1981)
<i>Picea rubens</i>	0.125	(Gordon 1981)
<i>Pinus banksiana</i>	0.286	(Gordon 1981)
<i>Pinus banksiana</i>	0.303	(Gordon 1981)

ENF	Mean = 0.26, std dev = 0.15, n = 129		(Continued)
<i>Pinus banksiana</i>	0.278	(Gordon 1981)	
<i>Pinus banksiana</i>	0.303	(Gordon 1981)	
<i>Pinus banksiana</i>	0.270	(Gordon 1981)	
<i>Pinus banksiana</i>	0.294	(Gordon 1981)	
<i>Pinus banksiana</i>	0.217	(Gordon 1981)	
<i>Pinus banksiana</i>	0.238	(Gordon 1981)	
<i>Pinus banksiana</i>	0.238	(Gordon 1981)	
<i>Pinus banksiana</i>	0.270	(Gordon 1981)	
<i>Pinus banksiana</i>	0.286	(Gordon 1981)	
<i>Pinus banksiana</i>	0.278	(Gordon 1981)	
<i>Pinus densiflora</i>	0.556	(Hatiya et al. 1965)	
<i>Pinus densiflora</i>	0.556	(Hatiya et al. 1965)	
<i>Pinus densiflora</i>	0.526	(Hatiya et al. 1965)	
<i>Pinus densiflora</i>	0.556	(Hatiya et al. 1965)	
<i>Pinus densiflora</i>	0.500	(Hatiya et al. 1965)	
<i>Pinus monticola</i>	0.385	(Hanley 1976)	
<i>Pinus monticola</i>	0.476	(Hanley 1976)	
<i>Pinus monticola</i>	0.333	(Hanley 1976)	
<i>Pinus monticola</i>	0.238	(Hanley 1976)	
<i>Pinus monticola</i>	0.385	(Hanley 1976)	
<i>Pinus monticola</i>	0.256	(Hanley 1976)	
<i>Pinus monticola</i>	0.256	(Hanley 1976)	
<i>Pinus monticola</i>	0.286	(Hanley 1976)	
<i>Pinus monticola</i>	0.256	(Hanley 1976)	
<i>Pinus monticola</i>	0.227	(Hanley 1976)	
<i>Pinus monticola</i>	0.244	(Hanley 1976)	
<i>Pinus monticola</i>	0.250	(Hanley 1976)	
<i>Pinus monticola</i>	0.278	(Hanley 1976)	
<i>Pinus monticola</i>	0.217	(Hanley 1976)	
<i>Pinus nigra</i>	0.417	(Minderman 1967)	
<i>Pinus nigra</i>	0.435	(Miller et al. 1976; Miller and Miller 1976)	
<i>Pinus nigra</i>	0.417	(Miller et al. 1976; Miller and Miller 1976)	
<i>Pinus nigra</i>	0.417	(Miller et al. 1976; Miller and Miller 1976)	
<i>Pinus nigra</i>	0.400	(Miller et al. 1976; Miller and Miller 1976)	
<i>Pinus nigra</i>	0.370	(Miller et al. 1976; Miller and Miller 1976)	
<i>Pinus pinea</i>	0.154	(Droste zu Hülshoff 1970; Ellenberg 1981a)	
<i>Pinus ponderosa</i>	0.417	(Whittaker and Niering 1968; Whittaker and Niering 1975)	
<i>Pinus ponderosa</i>	0.435	(Whittaker and Niering 1968; Whittaker and Niering 1975)	
<i>Pinus ponderosa</i>	0.476	(Whittaker and Niering 1968; Whittaker and Niering 1975)	
<i>Pinus ponderosa</i>	0.357	(Whittaker and Niering 1968; Whittaker and Niering 1975)	
<i>Pinus radiata</i>	0.333	(Forrest 1973; Forrest and Ovington 1970)	
<i>Pinus radiata</i>	0.294	(Forrest 1973; Forrest and Ovington 1970)	
<i>Pinus radiata</i>	0.588	(Forrest 1973; Forrest and Ovington 1970)	
<i>Pinus radiata</i>	0.476	(Forrest 1973; Forrest and Ovington 1970)	
<i>Pinus radiata</i>	0.500	(Madgwick et al. 1977a; Madgwick et al. 1977b)	
<i>Pinus radiata</i>	0.500	(Madgwick et al. 1977a; Madgwick et al. 1977b)	
<i>Pinus resinosa</i>	0.455	(Madgwick 1962; Madgwick et al. 1970)	
<i>Pinus rigida</i>	0.303	(Olsvig 1980)	
<i>Pinus rigida</i>	0.286	(Olsvig 1980)	

ENF	Mean = 0.26, std dev = 0.15, n = 129	(Continued)
<i>Pinus rigida</i>	0.278	(Olsvig 1980)
<i>Pinus rigida</i>	0.417	(Olsvig 1980)
<i>Pinus strobus</i>	0.769	(Swank and Schreuder 1973; Swank and Schreuder 1974)
<i>Pinus sylvestris</i>	0.385	(Mälkönen 1974)
<i>Pinus sylvestris</i>	0.400	(Mälkönen 1974)
<i>Pinus sylvestris</i>	0.400	(Mälkönen 1974)
<i>Pinus sylvestris</i>	0.345	(Alvera 1973; Alvera 1981)
<i>Pinus taeda</i>	1.00	(Nemeth 1973a; Nemeth 1973b)
<i>Pinus taeda</i>	0.435	(Nemeth 1973a; Nemeth 1973b)
<i>Pinus taeda</i>	0.556	(Nemeth 1973a; Nemeth 1973b)
<i>Pinus taeda</i>	0.435	(Nemeth 1973a; Nemeth 1973b)
<i>Pinus taeda</i>	0.909	(Ralston 1973)
<i>Pinus taeda</i>	0.588	(Wells et al. 1975)
<i>Pinus taeda</i>	0.476	(Nemeth 1973a; Nemeth 1973b)
<i>Pinus virginiana</i>	0.588	(Madgwick 1968)
<i>Pseudotsuga menziesii</i>	0.256	(Turner 1981; Turner and Long 1975)
<i>Pseudotsuga menziesii</i>	0.233	(Turner 1981; Turner and Long 1975)
<i>Pseudotsuga menziesii</i>	0.213	(Turner 1981; Turner and Long 1975)
<i>Pseudotsuga menziesii</i>	0.286	(Cole et al. 1968; Cole et al. 1981; Dice 1970; Grier et al. 1974)
<i>Pseudotsuga menziesii</i>	0.217	(Cole et al. 1968; Cole et al. 1981; Dice 1970; Grier et al. 1974)
<i>Pseudotsuga menziesii</i>	0.200	(Keyes and Grier 1981)
<i>Pseudotsuga menziesii</i>	0.200	(Keyes and Grier 1981)
<i>Pseudotsuga menziesii</i>	0.250	(Gholz 1982; Gholz et al. 1976; Gholz et al. 1979)
<i>Pseudotsuga menziesii</i>	0.250	(Gholz 1982; Gholz et al. 1976; Gholz et al. 1979)
<i>Pseudotsuga menziesii</i>	0.222	(Gholz 1982; Gholz et al. 1976; Gholz et al. 1979)
<i>Pseudotsuga menziesii</i>	0.417	(Turner 1981; Turner and Long 1975)
<i>Pseudotsuga menziesii</i>	0.500	(Turner 1981; Turner and Long 1975)
<i>Pseudotsuga menziesii</i>	0.323	(Turner 1981; Turner and Long 1975)
<i>Pseudotsuga menziesii</i>	0.270	(Turner 1981; Turner and Long 1975)
<i>Pseudotsuga menziesii</i>	0.213	(Whittaker and Niering 1968; Whittaker and Niering 1975)
<i>Pseudotsuga menziesii</i>	0.196	(Whittaker and Niering 1968; Whittaker and Niering 1975)
<i>Pseudotsuga menziesii</i>	0.313	(Gholz 1982; Gholz et al. 1976; Gholz et al. 1979)
<i>Tsuga diversifolia</i>	0.213	(Kitazawa 1981)
<i>Tsuga heterophylla</i>	0.294	(Fujimori 1971; Fujimori et al. 1976; Grier 1976)
<i>Tsuga heterophylla</i>	0.370	(Fujimori 1971; Fujimori et al. 1976; Grier 1976)
<i>Tsuga sieboldii</i>	0.294	(Ando et al. 1977)
DBF	1.00	Annual canopy turnover
DNF	1.00	Annual canopy turnover
Grass	1.00	Annual canopy turnover
Shrub	0.320	Set to ENF



### **A.1.2 Live wood turnover**

We are unaware of any appropriate data with which to parameterize live wood turnover (LWT,  $1 \text{ yr}^{-1}$ ). Since cambium (conceptually the live wood pool in BIOME-BGC) is replaced on an annual basis, LWT could be set to 1.0. However, since the living and respiring portion of the sapwood [primarily ray parenchyma (Kozlowski and Pallardy 1997)] originates from the cambium, some of the live wood must be retained, and we set LWT to 0.7 for all woody biomes.

### **A.1.3 Whole plant mortality**

Whole plant mortality (WPM,  $1 \text{ yr}^{-1}$ , including whole-tree death, branch shedding, herbivory, etc.) is the fraction of the above- and below-ground ecosystem carbon pools that dies or is consumed each year. Silvicultural researchers have collected large amounts of data on self-thinning processes and age–density relationships, but because BIOME-BGC requires a proportion of the stand (mass or volume) that dies each year in mature (not developing) stands, these data are not useable in the parameterization. Data in the required form are scarce. The forest value used here (0.0050) is based on a single ongoing large-scale field experiment being conducted by silvicultural researchers and is considered to represent mostly branch and tree mortality (R. E. Keane, USDA Forest Service, 1998, personal communication). Grass WPM (0.10) is meant to represent herbivory, which varies greatly with insect phenology and the presence or absence of grazing activity and can range from 0.06 in steppe (Lavrenko and Karamysheva 1992) to over 0.4 in savanna grasses (Gandar 1982). Our value is thus a low approximation. Shrub WPM (0.020) is set intermediate between the forest and grass biomes on the assumption that while there is a woody component to the biome, it is small enough that herbivory can still consume significant amounts.

### **A.1.4 Fire mortality**

Fire mortality ( $1 \text{ yr}^{-1}$ ) is based on approximations from data in Aber and Melillo (Aber and Melillo 1991). Based on their general co-occurrence, we set the DNF FM to the ENF value (0.0050). DBF FM is significantly lower (0.0025). Use of the low end of Aber and Melillo's (Aber and Melillo 1991) prairie fire regime of 0.1 resulted in extremely low simulated grass LAI and we reduced grass FM to 0.05. Data from grass-dominated tropical savannas suggest that FM of 0.05 (20-yr interval) is not uncommon (Lacey et al. 1982). To represent reduced fire rate in cold shrublands, we set shrub FM to 0.010, slightly below the low shrub value in Aber and Melillo (Aber and Melillo 1991).

## **A.2 Allocation parameters**

Allometric relationships between different plant pools control how photosynthetically produced carbon is allocated throughout the ecosystem. BIOME-BGC considers carbon allocation to major plant pools of roots (fine and coarse), stems, and leaves. The four ratios presented below are used in an algebraic solution to determine the allocation of carbon throughout the ecosystem. As each plant pool

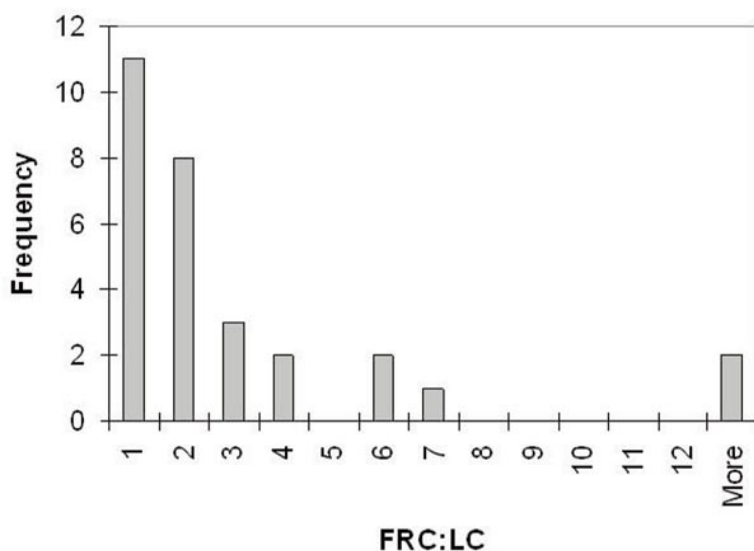


Figure A1. Frequency histogram of the ratio of new fine root carbon to new leaf carbon.

is associated with a fixed carbon to nitrogen ratio (below), allocation indirectly controls nitrogen demand.

Carbon allocation to seeds (Kaldy and Dunton 1999), fruit (Jonasson et al. 1997), and defensive chemistry (Crone and Jones 1999; Wallin and Raffa 1999) can represent a significant portion of total allocation, but the physiologic, genetic, and pathogenic detail required to accurately model these processes is impractical in a generalized ecosystem model. Site-specific application of BIOME-BGC or other BGC models should consider these processes.

The allocation parameters were, in general, well documented from a wealth of stand inventory data collected from the 1960s–1980s. However, little data were available for the DNF biome. DNF allocation exhibits similarities to both ENF and DBF patterns (Gower and Richards 1990) without complete justification for adopting either strategy as a surrogate for DNF. We arbitrarily chose to set DNF equal to ENF values.

### A.2.1 New fine root carbon to new leaf carbon allocation

In spite of the great difficulty in measuring FRC:LC ( $\text{kg C kg C}^{-1}$ ), there was a surprisingly large amount of data available, usually recorded separately as fine root and leaf NPP. The distribution of FRC:LC for ENF, upon which three biome values are based, was highly positively skewed, with the mean value (2.7) almost twice the median (Figure A1). Ratios close to one often produce skewed distributions because of the limited possible range of values less than one versus the unlimited range of values greater than one. Inverting the ratio to LC:FRC, for example, removes the skewness. Selecting the mean value also produced an indefensibly large allocation of carbon to fine roots. Even though nitrogen and water

were both available, LAI development with FRC:LC at the mean value was severely photosynthetically limited by fine root carbon consumption. With FRC:LC set at the mean, ENF did not grow an LAI above 1.9, even at relatively warm and wet sites two and four (appendix B). Thus, we used the median value. We also checked all other ratio values and found that ENF FRC:LC was the only case with extreme skewness.

ENF	Median = 1.4, pseudo-std dev = 1.5, $n = 29$	
<i>Abies</i>	12.4	(Vogt et al. 1982)
<i>Abies amabilis</i>	5.46	(Grier et al. 1981)
<i>Abies amabilis</i>	12.7	(Grier et al. 1981)
Mixed pine	0.931	(Nadelhoffer et al. 1985)
<i>Picea</i>	0.662	(Nadelhoffer et al. 1985)
<i>Pinus contorta</i>	3.64	(Comeau and Kimmins 1989)
<i>Pinus contorta</i>	5.50	(Comeau and Kimmins 1989)
<i>Pinus contorta</i>	2.76	(Comeau and Kimmins 1989)
<i>Pinus contorta</i>	1.47	(Comeau and Kimmins 1989)
<i>Pinus elliotii</i>	1.09	(Gholz et al. 1986)
<i>Pinus radiata</i>	0.463	(Beets and Pillock 1987)
<i>Pinus radiata</i>	0.347	(Beets and Pillock 1987)
<i>Pinus resinosa</i>	0.872	(Nadelhoffer et al. 1985)
<i>Pinus strobus</i>	0.994	(Nadelhoffer et al. 1985)
<i>Pinus sylvestris</i>	1.03	(Mälikönen 1974)
<i>Pinus sylvestris</i>	0.921	(Mälikönen 1974)
<i>Pinus sylvestris</i>	1.17	(Mälikönen 1974)
<i>Pinus sylvestris</i>	1.37	(Paavilainen 1980)
<i>Pinus sylvestris</i>	2.99	(Linder and Axelsson 1982)
<i>Pinus sylvestris</i>	0.523	(Linder and Axelsson 1982)
<i>Pinus taeda</i>	1.76	(Kinerson et al. 1977)
<i>Pseudotsuga menziesii</i>	3.66	(Keyes and Grier 1981)
<i>Pseudotsuga menziesii</i>	0.819	(Keyes and Grier 1981)
<i>Pseudotsuga menziesii</i>	1.41	(Vogt et al. 1990)
<i>Pseudotsuga menziesii</i>	0.883	(Vogt et al. 1990)
<i>Pseudotsuga menziesii</i>	2.41	(Gower et al. 1992)
<i>Pseudotsuga menziesii</i>	1.00	(Gower et al. 1992)
<i>Pseudotsuga menziesii</i>	1.43	(Gower et al. 1992)
<i>Pseudotsuga menziesii</i>	6.85	(Fogel 1983)
DNF	1.4	Set to ENF
DBF	Mean = 1.2, std dev = 1.2, $n = 9$	
<i>Quercus velutina</i>	1.59	(Nadelhoffer et al. 1985)
<i>Quercus rubra</i>	1.39	(Nadelhoffer et al. 1985)
<i>Quercus alba</i>	1.27	(Nadelhoffer et al. 1985)
<i>Acer saccharum</i>	1.55	(Nadelhoffer et al. 1985)
<i>Betula</i>	1.26	(Nadelhoffer et al. 1985)
<i>Fagus</i>	1.43	(van Praag et al. 1988)
<i>Quercus</i>	0.673	(Joslin and Henderson 1987)
<i>Fagus</i>	0.545	(Ellenberg et al. 1986)
<i>Nyssa-Acer</i>	1.44	(Symbula and Day 1988)
Grass	Mean = 1.0, std dev = 0.54, $n = 32$	
Salt marsh	1.00	(Bliss 1977)
Wet meadow	0.338	(Bliss 1977)

Grass	Mean = 1.0, std dev = 0.54, $n = 32$		(Continued)
Herb meadow	1.31	(Tieszen et al. 1981, see Lewis personal communication)	
Grass–herb meadow	1.01	(Østbye and et al. 1975)	
Dry grassland	2.19	(Lewis Smith and Walton 1975)	
Grass turf	0.500	(Collins et al. 1975)	
Grassland	2.00	(Jenkin 1975)	
Wet grassland	0.199	(Lewis Smith and Walton 1975)	
Dry meadow	1.02	(Wielgolaski 1975)	
Wet meadow	1.63	(Wielgolaski 1975)	
Grass savanna	1.59	(Menaut and Cesar 1979)	
Grass savanna	1.43	(Menaut and Cesar 1979)	
Grass savanna	1.32	(Menaut and Cesar 1979)	
Temperate grassland	1.07	(Sims and Coupland 1979)	
Temperate grassland	0.643	(Sims and Coupland 1979)	
Temperate grassland	0.405	(Sims and Coupland 1979)	
Temperate grassland	0.960	(Sims and Coupland 1979)	
Mixed grass	0.281	(Kumar and Joshi 1972)	
Mixed grass	0.470	(Singh and Yadava 1974)	
<i>Eragrostis</i>	0.342	(Singh 1972)	
<i>Desmostachya</i>	0.621	(Singh 1972)	
<i>Sehima-Heteropogon</i>	0.488	(Shankar et al. 1973)	
<i>Dichanthium</i>	0.892	(Misra 1973)	
<i>Sehima</i>	0.921	(Billore 1973)	
Mixed grass	1.29	(Naik 1973)	
<i>Heteropogon-Apluda-Cymbopogon</i>	1.03	(Jain 1971)	
Tropical grassland	1.78	(Singh et al. 1979)	
Tropical grassland	0.515	(Singh et al. 1979)	
Tropical grassland	1.00	(Singh et al. 1979)	
Tropical grassland	2.03	(Singh et al. 1979)	
Shortgrass steppe	0.988	(Milchunas and Laurenroth 1992)	
Konza prairie	0.744	(Hayes and Seastedt 1987)	
Shrub	1.4	Set to ENF	

### A.2.2 New stem carbon to new leaf carbon allocation

Extensive new stem carbon to new leaf carbon allocation (SC:LC, kg C kg C<sup>-1</sup>) data were available for ENF and DBF and showed identical values. However, preliminary testing showed that with shrub SC:LC set to 2.2, very large stem carbon accumulation occurred, and we reduced shrub SC:LC to 10% of the forest values.

ENF	Mean = 2.2, std dev = 0.89, $n = 29$	
<i>Abies amabilis</i>	3.58	(Gholz et al. 1976; Grier and Milne 1981; Grier et al. 1981)
<i>Abies amabilis</i>	3.37	(Gholz et al. 1976; Grier and Milne 1981; Grier et al. 1981)
<i>Abies balsamea</i>	1.02	(Baskerville 1965; Baskerville 1966)
<i>Abies balsamea</i>	1.14	(Baskerville 1965; Baskerville 1966)
<i>Abies balsamea</i>	1.13	(Baskerville 1965; Baskerville 1966)
<i>Abies balsamea</i>	1.16	(Baskerville 1965; Baskerville 1966)

ENF	Mean = 2.2, std dev = 0.89, n = 29	(Continued)
<i>Abies balsamea</i>	1.30	(Baskerville 1965; Baskerville 1966)
<i>Abies balsamea</i>	1.34	(Baskerville 1965; Baskerville 1966)
<i>Abies concolor</i>	1.69	(Whittaker and Niering 1968; Whittaker and Niering 1975)
<i>Abies fraseri</i>	2.29	(Whittaker 1966)
<i>Abies fraseri</i>	3.12	(Whittaker 1966)
<i>Abies fraseri</i>	1.61	(Whittaker 1966)
<i>Abies fraseri</i>	1.71	(Whittaker 1966)
<i>Abies lasiocarpa</i>	1.36	(Whittaker and Niering 1968; Whittaker and Niering 1975)
<i>Abies procera</i>	3.03	(Fujimori et al. 1976)
<i>Abies sachalinensis</i>	3.32	(Satoo 1973)
<i>Abies veitchii</i>	2.56	(Tadaki et al. 1967)
<i>Abies veitchii</i>	4.17	(Tadaki et al. 1967)
<i>Abies veitchii</i>	3.03	(Tadaki et al. 1967)
<i>Abies veitchii</i>	2.61	(Tadaki et al. 1967)
<i>Abies veitchii</i>	1.64	(Tadaki et al. 1967)
<i>Abies veitchii</i>	2.50	(Tadaki et al. 1967)
<i>Abies veitchii</i>	2.42	(Tadaki et al. 1967)
<i>Abies veitchii</i>	1.34	(Tadaki et al. 1967)
<i>Abies veitchii</i>	1.55	(Tadaki et al. 1967)
<i>Abies veitchii</i>	1.64	(Kimura 1963; Kimura 1969; Kimura et al. 1968)
<i>Abies veitchii</i>	1.62	(Kimura 1963; Kimura 1969; Kimura et al. 1968)
<i>Abies veitchii</i>	2.36	(Kimura 1963; Kimura 1969; Kimura et al. 1968)
<i>Abies veitchii</i>	2.37	(Kimura 1963; Kimura 1969; Kimura et al. 1968)
<i>Abies veitchii</i>	2.95	(Kimura 1963; Kimura 1969; Kimura et al. 1968)
<i>Abies veitchii</i>	3.20	(Kimura 1963; Kimura 1969; Kimura et al. 1968)
<i>Abies veitchii</i>	1.06	(Kimura 1963; Kimura 1969; Kimura et al. 1968)
<i>Picea abies</i>	4.70	(Duvigneaud and Kestemont 1977; Kestemont 1975)
<i>Picea abies</i>	1.76	(Droste zu Hülshoff 1970; Ellenberg 1981a)
<i>Picea abies</i>	1.43	(Droste zu Hülshoff 1970; Ellenberg 1981a)
<i>Picea abies</i>	1.45	(Droste zu Hülshoff 1970; Ellenberg 1981a)
<i>Picea abies</i>	2.68	(Satoo 1971)
<i>Picea abies</i>	1.51	(Satoo 1971)
<i>Picea abies</i>	1.48	(Satoo 1971)
<i>Picea abies</i>	2.35	(Satoo 1971)
<i>Picea abies</i>	2.09	(Satoo 1971; Yoshimura 1967)
<i>Picea abies</i>	3.42	(Nihlgard 1972; Nihlgard and Lindgren 1977; Nihlgard and Lindgren 1981)
<i>Picea rubens</i>	2.17	(Gordon 1981)
<i>Picea rubens</i>	1.24	(Gordon 1981)
<i>Picea rubens</i>	2.77	(Gordon 1981)
<i>Picea rubens</i>	2.34	(Gordon 1981)
<i>Pinus banksiana</i>	2.39	(Gordon 1981)
<i>Pinus banksiana</i>	2.45	(Gordon 1981)
<i>Pinus banksiana</i>	2.22	(Gordon 1981)
<i>Pinus banksiana</i>	2.22	(Gordon 1981)
<i>Pinus banksiana</i>	2.27	(Gordon 1981)
<i>Pinus banksiana</i>	2.19	(Gordon 1981)
<i>Pinus banksiana</i>	2.19	(Gordon 1981)
<i>Pinus banksiana</i>	2.16	(Gordon 1981)
<i>Pinus banksiana</i>	1.82	(Gordon 1981)



ENF	Mean = 2.2, std dev = 0.89, n = 29	(Continued)
<i>Pinus banksiana</i>	1.77	(Gordon 1981)
<i>Pinus banksiana</i>	1.46	(Gordon 1981)
<i>Pinus banksiana</i>	1.43	(Gordon 1981)
<i>Pinus densiflora</i>	2.50	(Hatiya et al. 1965)
<i>Pinus densiflora</i>	2.46	(Hatiya et al. 1965)
<i>Pinus densiflora</i>	2.21	(Hatiya et al. 1965)
<i>Pinus densiflora</i>	2.11	(Hatiya et al. 1965)
<i>Pinus densiflora</i>	3.18	(Hatiya et al. 1965)
<i>Pinus monticola</i>	0.613	(Hanley 1976)
<i>Pinus monticola</i>	0.596	(Hanley 1976)
<i>Pinus monticola</i>	0.932	(Hanley 1976)
<i>Pinus monticola</i>	0.934	(Hanley 1976)
<i>Pinus monticola</i>	2.26	(Hanley 1976)
<i>Pinus monticola</i>	2.55	(Hanley 1976)
<i>Pinus monticola</i>	2.24	(Hanley 1976)
<i>Pinus monticola</i>	2.11	(Hanley 1976)
<i>Pinus monticola</i>	0.704	(Hanley 1976)
<i>Pinus monticola</i>	2.35	(Hanley 1976)
<i>Pinus monticola</i>	2.03	(Hanley 1976)
<i>Pinus monticola</i>	1.90	(Hanley 1976)
<i>Pinus monticola</i>	2.33	(Hanley 1976)
<i>Pinus monticola</i>	2.46	(Hanley 1976)
<i>Pinus nigra</i>	1.53	(Minderman 1967)
<i>Pinus nigra</i>	2.09	(Miller et al. 1976; Miller and Miller 1976)
<i>Pinus nigra</i>	2.12	(Miller et al. 1976; Miller and Miller 1976)
<i>Pinus nigra</i>	2.10	(Miller et al. 1976; Miller and Miller 1976)
<i>Pinus nigra</i>	1.98	(Miller et al. 1976; Miller and Miller 1976)
<i>Pinus nigra</i>	1.70	(Miller et al. 1976; Miller and Miller 1976)
<i>Pinus pinea</i>	1.89	(Droste zu Hülshoff 1970; Ellenberg 1981a)
<i>Pinus ponderosa</i>	0.981	(Whittaker and Niering 1968; Whittaker and Niering 1975)
<i>Pinus ponderosa</i>	0.983	(Whittaker and Niering 1968; Whittaker and Niering 1975)
<i>Pinus ponderosa</i>	0.933	(Whittaker and Niering 1968; Whittaker and Niering 1975)
<i>Pinus ponderosa</i>	0.851	(Whittaker and Niering 1968; Whittaker and Niering 1975)
<i>Pinus radiata</i>	2.29	(Forrest 1973; Forrest and Ovington 197)
<i>Pinus radiata</i>	4.03	(Forrest 1973; Forrest and Ovington 1970)
<i>Pinus radiata</i>	3.59	(Forrest 1973; Forrest and Ovington 1970)
<i>Pinus radiata</i>	3.30	(Forrest 1973; Forrest and Ovington 1970)
<i>Pinus radiata</i>	2.08	(Madgwick et al. 1977a; Madgwick et al. 1977b)
<i>Pinus radiata</i>	2.28	(Madgwick et al. 1977a; Madgwick et al. 1977b)
<i>Pinus resinosa</i>	1.39	(Madgwick 1962; Madgwick et al. 1970)
<i>Pinus rigida</i>	1.61	(Olsvig 1980)
<i>Pinus rigida</i>	1.51	(Olsvig 1980)
<i>Pinus rigida</i>	1.99	(Olsvig 1980)
<i>Pinus rigida</i>	1.28	(Olsvig 1980)
<i>Pinus strobus</i>	2.73	(Swank and Schreuder 1973; Swank and Schreuder 1974)
<i>Pinus sylvestris</i>	1.80	(Mälkönen 1974)
<i>Pinus sylvestris</i>	2.07	(Mälkönen 1974)
<i>Pinus sylvestris</i>	2.11	(Mälkönen 1974)

ENF	Mean = 2.2, std dev = 0.89, $n = 29$		(Continued)
<i>Pinus sylvestris</i>	2.51	(Alvera 1973; Alvera 1981)	
<i>Pinus taeda</i>	2.05	(Nemeth 1973a; Nemeth 1973b)	
<i>Pinus taeda</i>	1.98	(Nemeth 1973a; Nemeth 1973b)	
<i>Pinus taeda</i>	3.61	(Nemeth 1973a; Nemeth 1973b)	
<i>Pinus taeda</i>	4.80	(Nemeth 1973a; Nemeth 1973b)	
<i>Pinus taeda</i>	1.99	(Ralston 1973)	
<i>Pinus taeda</i>	1.56	(Wells et al. 197)	
<i>Pinus taeda</i>	1.82	(Nemeth 1973a; Nemeth 1973b)	
<i>Pinus virginiana</i>	1.89	(Madgwick 1968)	
<i>Pseudotsuga</i>	1.65	(Turner 1981; Turner and Long 1975)	
<i>Pseudotsuga</i>	1.69	(Turner 1981; Turner and Long 1975)	
<i>Pseudotsuga</i>	1.24	(Turner 1981; Turner and Long 1975)	
<i>Pseudotsuga menziesii</i>	5.32	(Cole et al. 1968; Cole et al. 1981; Dice 1970; Grier et al. 1974)	
<i>Pseudotsuga menziesii</i>	3.95	(Cole et al. 1968; Cole et al. 1981; Dice 1970; Grier et al. 1974)	
<i>Pseudotsuga menziesii</i>	2.65	(Keyes and Grier 1981)	
<i>Pseudotsuga menziesii</i>	3.28	(Keyes and Grier 1981)	
<i>Pseudotsuga menziesii</i>	1.07	(Gholz 1982; Gholz et al. 1976; Gholz et al. 1979)	
<i>Pseudotsuga menziesii</i>	3.54	(Gholz 1982; Gholz et al. 1976; Gholz et al. 1979)	
<i>Pseudotsuga menziesii</i>	3.18	(Turner 1981; Turner and Long 1975)	
<i>Pseudotsuga menziesii</i>	1.68	(Turner 1981; Turner and Long 1975)	
<i>Pseudotsuga menziesii</i>	2.63	(Turner 1981; Turner and Long 1975)	
<i>Pseudotsuga menziesii</i>	3.17	(Turner 1981; Turner and Long 1975)	
<i>Pseudotsuga menziesii</i>	1.31	(Whittaker and Niering 1968; Whittaker and Niering 1975)	
<i>Pseudotsuga menziesii</i>	1.72	(Whittaker and Niering 1968; Whittaker and Niering 1975)	
<i>Pseudotsuga menziesii</i>	1.10	(Gholz 1982; Gholz et al. 1976; Gholz et al. 1979)	
<i>Pseudotsuga menziesii</i>	1.38	(Gholz 1982; Gholz et al. 1976; Gholz et al. 1979)	
<i>Tsuga diversifolia</i>	2.23	(Kitazawa 1981)	
<i>Tsuga heterophylla</i>	4.15	(Fujimori 1971; Fujimori et al. 1976; Grier 1976)	
<i>Tsuga heterophylla</i>	3.63	(Fujimori 1971; Fujimori et al. 1976; Grier 1976)	
<i>Tsuga sieboldii</i>	1.45	(Ando et al. 1977)	
DNF	2.2	Set to ENF	
DBF	Mean = 2.2, std dev = 1.1, $n = 133$		
<i>Acer platanoides</i>	2.46	(Hyttborn 1975)	
<i>Acer saccharum</i>	2.29	(Whittaker 1966; Whittaker 1971)	
<i>Acer saccharum</i>	2.29	(Whittaker 1966; Whittaker 1971)	
<i>Aesculus octandra</i>	3.03	(Whittaker 1966; Whittaker 1971)	
<i>Alnus glutinosa</i>	1.78	(Schlesinger 1978)	
<i>Alnus glutinosa</i>	3.48	(Nihlgard 1972; Nihlgard and Lindgren 1977; Nihlgard and Lindgren 1981)	
<i>Alnus incana</i>	1.83	(Whittaker 1966; Whittaker 1971)	
<i>Alnus rubra</i>	3.17	(van Cleve et al. 1971)	
<i>Alnus rubra</i>	1.85	(Zavitkovski et al. 1976; Zavitkovski and Stevens 1972)	
<i>Alnus rubra</i>	1.96	(Zavitkovski et al. 1976; Zavitkovski and Stevens 1972)	

DBF	Mean = 2.2, std dev = 1.1, n = 133	(Continued)
<i>Alnus rubra</i>	2.00	(Zavitkovski et al. 1976; Zavitkovski and Stevens 1972)
<i>Alnus rubra</i>	1.67	(Zavitkovski et al. 1976; Zavitkovski and Stevens 1972)
<i>Alnus rubra</i>	1.43	(Zavitkovski et al. 1976; Zavitkovski and Stevens 1972)
<i>Alnus rubra</i>	1.33	(Zavitkovski et al. 1976; Zavitkovski and Stevens 1972)
<i>Betula maximowicziana</i>	0.933	(Jakus 1981)
<i>Betula maximowicziana</i>	1.82	(Satoo 1970; Satoo 1974)
<i>Betula maximowicziana</i>	1.79	(Satoo 1970; Satoo 1974)
<i>Betula pubescens</i>	4.00	(Holm and Jensen 1981)
<i>Betula pubescens</i>	1.57	(Auclair and Méteyer 1980)
<i>Betula spp.</i>	0.920	(Decei 1981; Donita et al. 1981)
<i>Betula verrucosa</i>	2.78	(Hughes 1970; Hughes 1971)
<i>Betula verrucosa</i>	3.50	(Ovington and Madgwick 1959a; Ovington and Madgwick 1959b)
<i>Betula verrucosa</i>	4.25	(Ovington and Madgwick 1959a; Ovington and Madgwick 1959b)
<i>Betula verrucosa</i>	4.53	(Ovington and Madgwick 1959a; Ovington and Madgwick 1959b)
<i>Betula verrucosa</i>	4.86	(Ovington and Madgwick 1959a; Ovington and Madgwick 1959b)
<i>Betula verrucosa</i>	4.57	(Ovington and Madgwick 1959a; Ovington and Madgwick 1959b)
<i>Betula verrucosa</i>	4.92	(Ovington and Madgwick 1959a; Ovington and Madgwick 1959b)
<i>Betula verrucosa</i>	4.50	(Ovington and Madgwick 1959a; Ovington and Madgwick 1959b)
<i>Betula verrucosa</i>	4.20	(Ovington and Madgwick 1959a; Ovington and Madgwick 1959b)
<i>Betula verrucosa</i>	4.19	(Ovington and Madgwick 1959a; Ovington and Madgwick 1959b)
<i>Carpinus betulus</i>	1.41	(Mälikönen 1977)
<i>Carya spp.</i>	1.27	(Harris et al. 1973; Harris and Henderson 1981)
<i>Castanea sativa</i>	1.50	(Ford and Newbould 1970; Ford and Newbould 1971)
<i>Castanea sativa</i>	2.57	(Ford and Newbould 1970; Ford and Newbould 1971)
<i>Castanea sativa</i>	3.42	(Ford and Newbould 1970; Ford and Newbould 1971)
<i>Castanea sativa</i>	2.03	(Ford and Newbould 1970; Ford and Newbould 1971)
<i>Fagus crenata</i>	2.15	(Satoo 1970; Satoo 1974)
<i>Fagus crenata</i>	2.06	(Tadaki et al. 1969)
<i>Fagus crenata</i>	2.34	(Tadaki et al. 1969)
<i>Fagus crenata</i>	2.43	(Tadaki et al. 1969)
<i>Fagus crenata</i>	1.17	(Kakubari 1977)
<i>Fagus crenata</i>	1.20	(Kakubari 1977)
<i>Fagus crenata</i>	1.51	(Kakubari 1977)
<i>Fagus crenata</i>	0.869	(Kakubari 1977)
<i>Fagus crenata</i>	0.746	(Kakubari 1977)
<i>Fagus crenata</i>	0.685	(Kakubari 1977)

DBF	Mean = 2.2, std dev = 1.1, n = 133	(Continued)
<i>Fagus crenata</i>	0.827	(Kakubari 1977)
<i>Fagus crenata</i>	0.747	(Kakubari 1977)
<i>Fagus crenata</i>	1.80	(Maruyama 1971; Maruyama 1977)
<i>Fagus crenata</i>	1.81	(Maruyama 1971; Maruyama 1977)
<i>Fagus crenata</i>	2.25	(Maruyama 1971; Maruyama 1977)
<i>Fagus crenata</i>	2.02	(Maruyama 1971; Maruyama 1977)
<i>Fagus crenata</i>	1.73	(Maruyama 1971; Maruyama 1977)
<i>Fagus crenata</i>	2.08	(Maruyama 1971; Maruyama 1977)
<i>Fagus crenata</i>	1.36	(Maruyama 1971; Maruyama 1977)
<i>Fagus crenata</i>	1.68	(Maruyama 1971; Maruyama 1977)
<i>Fagus crenata</i>	1.31	(Maruyama 1971; Maruyama 1977)
<i>Fagus crenata</i>	3.11	(Kawahara et al. 1979; Ogino 1977)
<i>Fagus grandifolia</i>	2.37	(Turner et al. 1976)
<i>Fagus grandifolia</i>	1.58	(Bormann et al. 1970; Gosz et al. 1972; Whittaker et al. 1974)
<i>Fagus grandifolia</i>	1.82	(Bormann et al. 1970; Gosz et al. 1972; Whittaker et al. 1974)
<i>Fagus grandifolia</i>	1.87	(Bormann et al. 1970; Gosz et al. 1972; Whittaker et al. 1974)
<i>Fagus grandifolia</i>	1.10	(Whittaker 1966; Whittaker 1971; Young 1972)
<i>Fagus sylvatica</i>	3.88	(Kestemont 1975)
<i>Fagus sylvatica</i>	2.84	(Duvigneaud and Kestemont 1977; Kestemont 1975)
<i>Fagus sylvatica</i>	0.533	(Pollard 1972)
<i>Fagus sylvatica</i>	2.00	(Auclair and Méteyer 1980)
<i>Fagus sylvatica</i>	1.83	(Lemée 1978)
<i>Fagus sylvatica</i>	2.80	(Ellenberg 1971; Ellenberg 1981b)
<i>Fagus sylvatica</i>	2.02	(Ellenberg 1971; Ellenberg 1981b)
<i>Fagus sylvatica</i>	2.39	(Hytteborn 1975)
<i>Fagus sylvatica</i>	3.39	(Nihlgard 1972; Nihlgard and Lindgren 1977; Nihlgard and Lindgren 1981)
<i>Fagus sylvatica</i>	3.22	(Nihlgard 1972; Nihlgard and Lindgren 1977; Nihlgard and Lindgren 1981)
<i>Liriodendron tulipifera</i>	1.22	(Whittaker 1966; Whittaker 1971; Young 1972)
<i>Liriodendron tulipifera</i>	4.85	(Whittaker 1966)
<i>Liriodendron tulipifera</i>	0.608	(Harris et al. 1977; Reichle et al. 1981; Sollins et al. 1973)
<i>Populus davidiana</i>	1.82	(Kawahara et al. 1979; Ogino 1977)
<i>Populus grandidentata</i>	0.910	(Harris et al. 1973; Harris and Henderson 1981)
<i>Populus grandidentata</i>	3.58	(Koerper and Richardson 1980)
<i>Populus grandidentata</i>	3.13	(Koerper and Richardson 1980)
<i>Populus tremuloides</i>	2.05	(Koerper and Richardson 1980)
<i>Populus tremuloides</i>	0.706	(Bray and Dudkiewicz 1963; Gosz 1980)
<i>Populus tremuloides</i>	1.75	(Alban and Niering 1975; Whittaker and Niering 1975)
<i>Populus tremuloides</i>	3.36	(Alban and Niering 1975; Whittaker and Niering 1975)
<i>Populus tremuloides</i>	2.45	(Crow 1978)
<i>Populus tremuloides</i>	1.69	(Crow 1978)
<i>Populus tremuloides</i>	2.42	(Kestemont 1971; Kestemont 1975)
<i>Populus tremuloides</i>	2.77	(Pollard 1972)
<i>Populus tremuloides</i>	2.38	(Pollard 1972)
<i>Quercus</i>	5.28	(Whittaker 1963; Whittaker 1966)

DBF	Mean = 2.2, std dev = 1.1, $n = 133$		(Continued)
<i>Quercus alba</i>	1.03	(Crow 1978)	
<i>Quercus alba</i>	1.36	(Lawson et al. 1981)	
<i>Quercus alba</i>	1.09	(Lawson et al. 1981)	
<i>Quercus alba</i>	0.800	(Rochow 1974a; Rochow 1974b; Rochow 1975; Whittaker 1966)	
<i>Quercus borealis</i>	3.43	(Rochow 1974a; Rochow 1974b; Rochow 1975; Whittaker 1966)	
<i>Quercus borealis</i>	1.68	(Ovington et al. 1963; Whittaker 1963; Whittaker 1966)	
<i>Quercus ellipsoidalis</i>	1.17	(Ovington et al. 1963; Whittaker 1963; Whittaker 1966)	
<i>Quercus oblongifolia</i>	1.85	(Reiners 1972; Reiners and Reiners 1970; Whittaker and Niering 1975)	
<i>Quercus pedunculiflora</i>	0.803	(Decei 1981; Donita et al. 1981)	
<i>Quercus petraea</i>	2.89	(Duvigneaud and Kestemont 1977; Kestemont 1975)	
<i>Quercus petraea</i>	1.73	(Duvigneaud and Froment 1969; Duvigneaud and Kestemont 1977; Duvigneaud et al. 1971)	
<i>Quercus petraea</i>	2.70	(Ellenberg 1971; Ellenberg 1981b)	
<i>Quercus petraea</i>	3.00	(Satoo 1970; Satoo et al. 1956)	
<i>Quercus prinus</i>	1.57	(Reiners 1972; Reiners and Reiners 1970; Whittaker and Niering 1975)	
<i>Quercus prinus</i>	3.33	(Whittaker 1963; Whittaker 1966)	
<i>Quercus prinus</i>	1.32	(Harris et al. 1973; Harris and Henderson 1981)	
<i>Quercus pubescens</i>	1.90	(van der Drift 1974; van der Drift 1981)	
<i>Quercus robur</i>	2.60	(Duvigneaud and Froment 1969; Duvigneaud and Kestemont 1977; Duvigneaud et al. 1971)	
<i>Quercus robur</i>	2.11	(Duvigneaud and Froment 1969; Duvigneaud and Kestemont 1977; Duvigneaud et al. 1971)	
<i>Quercus robur</i>	1.79	(Duvigneaud and Froment 1969; Duvigneaud and Kestemont 1977; Duvigneaud et al. 1971)	
<i>Quercus robur</i>	2.66	(Kestemont 1971; Kestemont 1975)	
<i>Quercus robur</i>	2.01	(Hyttborn 1975)	
<i>Quercus stellata</i>	1.32	(Day and Monk 1977a; Day and Monk 1977b; Day and Monk 1974)	
<i>Taxodium distichum</i>	1.65	(Johnson and Risser 1974)	
Grass	No woody component		
Shrub	0.22	See text for discussion	

### A.2.3 New live wood carbon to new total wood carbon allocation

New live wood carbon to new total wood carbon allocation (LWC:TWC,  $\text{kg C kg C}^{-1}$ ) controls the amount of respiring tissue in new wood and is based on the percentage of living parenchyma cells in sapwood. For shrubs we assumed that all stem carbon is live. Since only the living portion of wood is respiring, LWC:TWC is important for stem respiration predictions.

ENF	Mean = 0.071, std dev = 0.014, $n = 8$	
<i>Abies balsamea</i>	0.0560	(Panshin et al. 1964)
<i>Larix occidentalis</i>	0.100	(Panshin et al. 1964)
<i>Picea engelmannii</i>	0.0590	(Panshin et al. 1964)



ENF	Mean = 0.071, std dev = 0.014, $n = 8$		(Continued)
<i>Pinus taeda</i>	0.0760	(Panshin et al. 1964)	
<i>Pseudotsuga menziesii</i>	0.0730	(Panshin et al. 1964)	
<i>Sequoia sempervirens</i>	0.0780	(Panshin et al. 1964)	
<i>Taxodium distichum</i>	0.0660	(Panshin et al. 1964)	
<i>Tsuga canadensis</i>	0.0590	(Panshin et al. 1964)	
DNF	0.071	Set to ENF	
DBF	Mean = 0.16, std dev = 0.084, $n = 8$		
<i>Acer saccharum</i>	0.179	(Panshin et al. 1964)	
<i>Betula alleghaniensis</i>	0.107	(Panshin et al. 1964)	
<i>Fagus grandifolia</i>	0.204	(Panshin et al. 1964)	
<i>Liriodendron tulipifera</i>	0.142	(Panshin et al. 1964)	
<i>Populus tremuloides</i>	0.096	(Panshin et al. 1964)	
<i>Quercus alba</i>	0.279	(Panshin et al. 1964)	
<i>Robinia pseudoacacia</i>	0.209	(Panshin et al. 1964)	
<i>Tilia americana</i>	0.00600	(Panshin et al. 1964)	
Grass	No woody component		
Shrub	1.0	See text for discussion	

#### A.2.4 Coarse root carbon to stem carbon allocation

Coarse root carbon to stem carbon allocation (CRC:SC, kg C kg C<sup>-1</sup>) was well documented and similar between the ENF and DBF biomes. Together with FRC:LC, CRC:SC is important for determining the mass and respiration of above- and below-ground portions of the ecosystem.

ENF	Mean = 0.29, std dev = 0.14, $n = 56$	
<i>Abies amabilis</i>	0.395	(Gholz et al. 1979; Grier and Milne 1981; Grier et al. 1981)
<i>Abies amabilis</i>	0.202	(Gholz et al. 1979; Grier and Milne 1981; Grier et al. 1981)
<i>Abies veitchii</i>	0.659	(Tadaki et al. 1967)
<i>Abies veitchii</i>	0.298	(Tadaki et al. 1967)
<i>Abies veitchii</i>	0.301	(Tadaki et al. 1967)
<i>Abies veitchii</i>	0.302	(Tadaki et al. 1967)
<i>Abies veitchii</i>	0.488	(Tadaki et al. 1970)
<i>Abies veitchii</i>	0.318	(Tadaki et al. 1970)
<i>Abies veitchii</i>	0.413	(Tadaki et al. 1970)
<i>Abies veitchii</i>	0.273	(Tadaki et al. 1970)
<i>Abies veitchii</i>	0.235	(Tadaki et al. 1970)
<i>Abies veitchii</i>	0.266	(Kimura 1963; Kimura 1969; Kimura et al. 1968)
<i>Picea abies</i>	0.159	(Duvigneaud and Kestemont 1977; Kestemont 1975)
<i>Picea abies</i>	0.194	(Droste zu Hülshoff 1970; Ellenberg 1981b)
<i>Picea abies</i>	0.230	(Nihlgard 1972; Nihlgard and Lindgren 1977; Nihlgard and Lindgren 1981)
<i>Pinus densiflora</i>	0.236	(Hatiya et al. 1965)
<i>Pinus densiflora</i>	0.246	(Hatiya et al. 1965)
<i>Pinus densiflora</i>	0.240	(Hatiya et al. 1965)
<i>Pinus densiflora</i>	0.238	(Hatiya et al. 1965)
<i>Pinus densiflora</i>	0.259	(Hatiya et al. 1965)

ENF	Mean = 0.29, std dev = 0.14, n = 56		(Continued)
<i>Pinus monticola</i>	0.211	(Hanley 1976)	
<i>Pinus monticola</i>	0.250	(Hanley 1976)	
<i>Pinus monticola</i>	0.171	(Hanley 1976)	
<i>Pinus monticola</i>	0.367	(Hanley 1976)	
<i>Pinus monticola</i>	0.483	(Hanley 1976)	
<i>Pinus monticola</i>	0.186	(Hanley 1976)	
<i>Pinus monticola</i>	0.200	(Hanley 1976)	
<i>Pinus monticola</i>	0.165	(Hanley 1976)	
<i>Pinus monticola</i>	0.184	(Hanley 1976)	
<i>Pinus monticola</i>	0.213	(Hanley 1976)	
<i>Pinus monticola</i>	0.203	(Hanley 1976)	
<i>Pinus monticola</i>	0.187	(Hanley 1976)	
<i>Pinus monticola</i>	0.173	(Hanley 1976)	
<i>Pinus monticola</i>	0.174	(Hanley 1976)	
<i>Pinus nigra</i>	0.220	(Miller et al. 1976; Miller and Miller 1976)	
<i>Pinus nigra</i>	0.515	(Miller et al. 1976; Miller and Miller 1976)	
<i>Pinus nigra</i>	0.303	(Miller et al. 1976; Miller and Miller 1976)	
<i>Pinus nigra</i>	0.264	(Miller et al. 1976; Miller and Miller 1976)	
<i>Pinus nigra</i>	0.471	(Miller et al. 1976; Miller and Miller 1976)	
<i>Pinus pinea</i>	0.288	(Droste zu Hülshoff 1970; Ellenberg 1981b)	
<i>Pinus sylvestris</i>	0.593	(Mälikönen 1974)	
<i>Pinus sylvestris</i>	0.375	(Mälikönen 1974)	
<i>Pinus sylvestris</i>	0.351	(Mälikönen 1974)	
<i>Pinus taeda</i>	0.221	(Nemeth 1973a; Nemeth 1973b)	
<i>Pinus taeda</i>	0.228	(Nemeth 1973a; Nemeth 1973b)	
<i>Pinus taeda</i>	0.182	(Nemeth 1973a; Nemeth 1973b)	
<i>Pinus taeda</i>	0.181	(Nemeth 1973a; Nemeth 1973b)	
<i>Pinus taeda</i>	0.841	(Harris et al. 1977; Kinerson et al. 1977; Ralston 1973)	
<i>Pinus taeda</i>	0.250	(Nemeth 1973a; Nemeth 1973b)	
<i>Pseudotsuga menziesii</i>	0.310	(Cole et al. 1968; Cole et al. 1981; Dice 1970; Grier et al. 1974)	
<i>Pseudotsuga menziesii</i>	0.151	(Cole et al. 1968; Cole et al. 1981; Dice 1970; Grier et al. 1974)	
<i>Pseudotsuga menziesii</i>	0.472	(Keyes and Grier 1981)	
<i>Pseudotsuga menziesii</i>	0.257	(Keyes and Grier 1981)	
<i>Tsuga heterophylla</i>	0.214	(Fujimori 1971; Fujimori et al. 1976; Grier 1976)	
<i>Tsuga heterophylla</i>	0.248	(Fujimori 1971; Fujimori et al. 1976; Grier 1976)	
<i>Tsuga sieboldii</i>	0.181	(Ando et al. 1977)	
DNF	0.29	Set to ENF	
<hr/>			
DBF	Mean = 0.22, std dev = 0.18, n = 46		
<i>Aesculus octandra</i>	0.247	(Whittaker 1966; Whittaker 1971)	
<i>Alnus glutinosa</i>	0.161	(Kestemont 1975)	
<i>Alnus rubra</i>	0.274	(Zavitkovski et al. 1976; Zavitkovski and Stevens 1972)	
<i>Betula pubescens</i>	0.452	(Mälikönen 1977)	
<i>Betula pubescens</i>	0.127	(Lemée 1978)	
<i>Fagus crenata</i>	0.162	(Tadaki et al. 1969)	
<i>Fagus crenata</i>	0.227	(Tadaki et al. 1969)	
<i>Fagus crenata</i>	0.134	(Tadaki et al. 1969)	
<i>Fagus crenata</i>	0.165	(Kakubari 1977)	
<i>Fagus crenata</i>	0.168	(Kakubari 1977)	

DBF	Mean = 0.22, std dev = 0.18, n = 46		(Continued)
<i>Fagus crenata</i>	0.178	(Kakubari 1977)	
<i>Fagus crenata</i>	0.142	(Kakubari 1977)	
<i>Fagus crenata</i>	0.126	(Kakubari 1977)	
<i>Fagus crenata</i>	0.160	(Kakubari 1977)	
<i>Fagus crenata</i>	0.144	(Kakubari 1977)	
<i>Fagus crenata</i>	0.134	(Kakubari 1977)	
<i>Fagus crenata</i>	0.311	(Maruyama 1971; Maruyama 1977)	
<i>Fagus crenata</i>	0.310	(Maruyama 1971; Maruyama 1977)	
<i>Fagus crenata</i>	0.288	(Maruyama 1971; Maruyama 1977)	
<i>Fagus crenata</i>	0.299	(Maruyama 1971; Maruyama 1977)	
<i>Fagus crenata</i>	0.316	(Maruyama 1971; Maruyama 1977)	
<i>Fagus crenata</i>	0.297	(Maruyama 1971; Maruyama 1977)	
<i>Fagus crenata</i>	0.336	(Maruyama 1971; Maruyama 1977)	
<i>Fagus crenata</i>	0.319	(Maruyama 1971; Maruyama 1977)	
<i>Fagus crenata</i>	0.354	(Maruyama 1971; Maruyama 1977)	
<i>Fagus crenata</i>	0.231	(Kawahara et al. 1979; Ogino 1977)	
<i>Fagus grandifolia</i>	0.310	(Bormann et al. 1970; Gosz et al. 1972; Whittaker et al. 1974)	
<i>Fagus grandifolia</i>	0.315	(Bormann et al. 1970; Gosz et al. 1972; Whittaker et al. 1974)	
<i>Fagus grandifolia</i>	0.319	(Bormann et al. 1970; Gosz et al. 1972; Whittaker et al. 1974)	
<i>Fagus sylvatica</i>	0.161	(Duvigneaud and Kestemont 1977; Kestemont 1975)	
<i>Fagus sylvatica</i>	0.216	(Duvigneaud and Kestemont 1977; Kestemont 1975)	
<i>Fagus sylvatica</i>	0.135	(Ellenberg 1971; Ellenberg 1981b)	
<i>Fagus sylvatica</i>	0.090	(Ellenberg 1971; Ellenberg 1981b)	
<i>Fagus sylvatica</i>	0.077	(Ellenberg 1971; Ellenberg 1981b)	
<i>Fagus sylvatica</i>	0.197	(Nihlgard 1972; Nihlgard and Lindgren 1977)	
<i>Fagus sylvatica</i>	0.174	(Nihlgard 1972; Nihlgard and Lindgren 1977)	
<i>Fagus sylvatica</i>	0.181	(Nihlgard 1972; Nihlgard and Lindgren 1977)	
<i>Liriodendron tulipifera</i>	0.563	(Harris et al. 1973; Harris and Henderson 1981)	
<i>Populus tremuloides</i>	0.152	(Pastor and Bockheim 1981)	
<i>Quercus petraea</i>	0.185	(Duvigneaud and Froment 1969; Duvigneaud and Kestemont 1977; Duvigneaud et al. 1971)	
<i>Quercus petraea</i>	0.101	(Duvigneaud and Froment 1969; Duvigneaud and Kestemont 1977; Duvigneaud et al. 1971)	
<i>Quercus petraea</i>	0.264	(van der Drift 1974; van der Drift 1981)	
<i>Quercus robur</i>	0.096	(Duvigneaud and Froment 1969; Duvigneaud and Kestemont 1977; Duvigneaud et al. 1971)	
<i>Quercus robur</i>	0.187	(Duvigneaud and Froment 1969; Duvigneaud and Kestemont 1977; Duvigneaud et al. 1971)	
<i>Quercus robur</i>	0.157	(Kestemont 1971; Kestemont 1975)	
<i>Quercus robur</i>	0.195	(Kestemont 1971; Kestemont 1975)	
Grass	No woody component		
Shrub	0.29	Set to ENF	

### A.3 Carbon to nitrogen parameters

The ratio of carbon to nitrogen (C:N) is used to characterize the nutrient concentration of leaf, litter, fine root, live wood, and dead wood pools. Usually measured

as milligrams of nitrogen per gram of dry weight or percent nitrogen, C:N is commonly measured and exerts strong control over plant nitrogen demand, decomposition, and respiration.

### A.3.1 Leaf carbon to nitrogen ratio

Leaf carbon to nitrogen ratio ( $C:N_{\text{leaf}}$ ,  $\text{kg C kg N}^{-1}$ ) determines three important factors: the nitrogen required to construct leaves (thus LAI), the amount of nitrogen available for investment in photosynthetic machinery (also controlled by PLNR, see below), and leaf respiration rates.

ENF	Mean = 42, std dev = 11, $n = 25$	
<i>Juniperus virginia</i>	30.5	(Reich et al. 1995a)
<i>Picea abies</i>	58.8	(Berg 1988)
<i>Picea abies</i>	28.1	(Reich et al. 1995a)
<i>Picea glauca</i>	40.3	(Reich et al. 1995a)
<i>Picea mariana</i>	41.3	(Reich et al. 1995a)
<i>Pinus albicaulis</i>	45.4	(Gower and Richards 1990)
<i>Pinus banksiana</i>	40.3	(Reich et al. 1995a)
<i>Pinus contorta</i>	51.0	(Hunt et al. 1988)
<i>Pinus contorta</i>	70.0	(Fahey et al. 1985)
<i>Pinus contorta</i>	47.6	(Berg and Ekhhom 1991)
<i>Pinus contorta</i>	35.7	(Gower et al. 1987)
<i>Pinus contorta</i>	41.6	(Gower and Richards 1990)
<i>Pinus resinosa</i>	37.0	(Reich et al. 1995a)
<i>Pinus resinosa</i>	50.0	(Reich et al. 1995a)
<i>Pinus strobus</i>	29.4	(Reich et al. 1995a)
<i>Pinus strobus</i>	22.8	(Reich et al. 1995a)
<i>Pinus sylvestris</i>	33.1	(Berg 1988)
<i>Pinus sylvestris</i>	36.0	(Reich et al. 1995a)
<i>Pinus sylvestris</i>	33.1	(Berg and Ekhhom 1991)
<i>Pinus taeda</i>	42.0	(Naidu et al. 1993)
<i>Pseudotsuga menziesii</i>	50.0	(Brix 1981)
<i>Pseudotsuga menziesii</i>	40.0	(Mitchell and Hinckley 1993)
<i>Thuja occidentalis</i>	58.1	(Reich et al. 1995a)
<i>Thuja occidentalis</i>	39.1	(Reich et al. 1995a)
<i>Tsuga mertensiana</i>	41.6	(Gower and Richards 1990)
DNF	Mean = 27, std dev = 5.6, $n = 30$	
<i>Larix decidua</i>	26.0	(Kloppel et al. 1998)
<i>Larix decidua</i>	27.8	(Kloppel et al. 1998)
<i>Larix decidua</i>	33.6	(Kloppel et al. 1998)
<i>Larix decidua</i>	26.3	(Kloppel et al. 1998)
<i>Larix decidua</i>	29.8	(Kloppel et al. 1998)
<i>Larix decidua</i>	23.7	(Kloppel et al. 1998)
<i>Larix decidua</i>	18.9	(Kloppel et al. 1998)
<i>Larix decidua</i>	20.0	(Matyssek and Schulze 1987)
<i>Larix eurolepis</i>	16.7	(Matyssek and Schulze 1987)
<i>Larix gmelinii</i>	28.1	(Kloppel et al. 1998)
<i>Larix laricina</i>	30.3	(Kloppel et al. 1998)
<i>Larix laricina</i>	33.8	(Kloppel et al. 1998)
<i>Larix laricina</i>	20.9	(Kloppel et al. 1998)
<i>Larix laricina</i>	37.0	(Kloppel et al. 1998)
<i>Larix leptolepis</i>	20.8	(Matyssek and Schulze 1987)

DNF	Mean = 27, std dev = 5.6, $n = 30$		(Continued)
<i>Larix lyallii</i>	22.1	(Kloeppe et al. 1998)	
<i>Larix lyallii</i>	23.8	(Gower and Richards 1990)	
<i>Larix lyallii</i>	27.8	(Richards 1981)	
<i>Larix occidentalis</i>	24.4	(Kloeppe et al. 1998)	
<i>Larix occidentalis</i>	25.3	(Kloeppe et al. 1998)	
<i>Larix occidentalis</i>	34.7	(Kloeppe et al. 1998)	
<i>Larix occidentalis</i>	35.2	(Kloeppe et al. 1998)	
<i>Larix occidentalis</i>	32.3	(Kloeppe et al. 1998)	
<i>Larix occidentalis</i>	31.3	(Kloeppe et al. 1998)	
<i>Larix occidentalis</i>	25.0	(Gower 1987)	
<i>Larix occidentalis</i>	29.4	(Gower and Richards 1990)	
<i>Larix olgenis</i>	32.7	(Kloeppe et al. 1998)	
<i>Larix siberica</i>	20.2	(Kloeppe et al. 1998)	
<i>Larix siberica</i>	22.3	(Kloeppe et al. 1998)	
<i>Larix siberica</i>	18.6	(Kloeppe et al. 1998)	
DBF	Mean = 25, std dev = 5.4, $n = 43$		
<i>Acer rubrum</i>	23.8	(Reich et al. 1995a)	
<i>Acer rubrum</i>	25.6	(Reich et al. 1995a)	
<i>Acer saccharum</i>	25.6	(Reich et al. 1995a)	
<i>Acer saccharum</i>	28.6	(Reich et al. 1995a)	
<i>Acer saccharum</i>	32.5	(Ellsworth and Reich 1992a)	
<i>Acer saccharum</i>	23.5	(Ellsworth and Reich 1992a)	
<i>Acer saccharum</i>	25.8	(Ellsworth and Reich 1992a)	
<i>Acer saccharum</i>	31.1	(Jose and Gillespie 1996)	
<i>Alnus glutinosa</i>	18.5	(Dawson and Funk 1981)	
<i>Alnus incana</i>	16.3	(Berg and Ekholm 1991)	
<i>Betula nigra</i>	21.9	(Reich et al. 1995a)	
<i>Betula papyrifera</i>	28.7	(Berg and Ekholm 1991)	
<i>Betula pumila</i>	33.1	(Reich et al. 1995a)	
<i>Carya glabra</i>	33.1	(Jose and Gillespie 1996)	
<i>Carya ovata</i>	25.2	(Reich et al. 1995a)	
<i>Catalpa speciosa</i>	27.0	(Reich et al. 1995a)	
<i>Celtis occidentalis</i>	20.9	(Reich et al. 1995a)	
<i>Cornus florida</i>	35.7	(Reich et al. 1995a)	
<i>Fagus grandifolia</i>	26.9	(Jose and Gillespie 1996)	
<i>Fraxinus americana</i>	23.5	(Reich et al. 1995a)	
<i>Fraxinus americana</i>	23.5	(Reich et al. 1995a)	
<i>Ilex verticillata</i>	32.3	(Reich et al. 1995a)	
<i>Juglans nigra</i>	16.9	(Reich et al. 1995a)	
<i>Liriodendron tulipifera</i>	31.4	(Jose and Gillespie 1996)	
<i>Lonicera x bella</i>	26.9	(Reich et al. 1995a)	
<i>Morus rubra</i>	21.6	(Reich et al. 1995a)	
<i>Populus deltoides</i>	21.2	(Reich et al. 1995a)	
<i>Populus tremuloides</i>	22.6	(Reich et al. 1995a)	
<i>Prunus serotina</i>	24.2	(Reich et al. 1995a)	
<i>Prunus serotina</i>	18.9	(Reich et al. 1995a)	
<i>Quercus alba</i>	27.2	(Jose and Gillespie 1996)	
<i>Quercus ellipsoidalis</i>	23.8	(Reich et al. 1995a)	
<i>Quercus macrocarpa</i>	21.3	(Reich et al. 1995a)	
<i>Quercus prinus</i>	35.0	(Jose and Gillespie 1996)	
<i>Quercus rubra</i>	16.8	(Reich et al. 1995a)	
<i>Quercus rubra</i>	23.7	(Reich et al. 1995a)	

DBF	Mean = 25, std dev = 5.4, n = 43		(Continued)
<i>Quercus rubra</i>	33.1	(Jose and Gillespie 1996)	
<i>Quercus velutina</i>	34.0	(Jose and Gillespie 1996)	
<i>Rhamnus cathartica</i>	21.6	(Reich et al. 1995a)	
<i>Rubus alleghaniensis</i>	16.5	(Reich et al. 1995a)	
<i>Salix dasyclados</i>	18.7	(Kull et al. 1998)	
<i>Salix viminalis</i>	20.6	(Kull et al. 1998)	
<i>Ulmus americana</i>	25.9	(Reich et al. 1995a)	
Grass	Mean = 25, std dev = 8.6, n = 47		
<i>Aegilops ovata</i>	17.7	(Garnier et al. 1997)	
<i>Agropyron smithii</i>	28.1	(Hunt et al. 1988)	
<i>Agropyron sp.</i>	14.3	(Garnier et al. 1997)	
<i>Andropogon gerardii</i>	32.9	(Knapp 1985)	
<i>Andropogon gerardii</i>	58.8	(Knapp 1985)	
<i>Avena barbata</i>	18.9	(Garnier et al. 1997)	
<i>Avenula bromoides</i>	24.8	(Garnier et al. 1997)	
<i>Brachypodium distachyon</i>	29.0	(Garnier et al. 1997)	
<i>Brachypodium phoenicoides</i>	30.8	(Garnier et al. 1997)	
<i>Brachypodium phoenicoides</i>	32.5	(Garnier et al. 1997)	
<i>Brachypodium retusum</i>	24.6	(Garnier et al. 1997)	
<i>Brachypodium retusum</i>	27.9	(Garnier et al. 1997)	
<i>Bromus erectus</i>	27.3	(Garnier et al. 1997)	
<i>Bromus erectus</i>	23.2	(Garnier et al. 1997)	
<i>Bromus erectus</i>	23.8	(Garnier et al. 1997)	
<i>Bromus hordeadeus</i>	18.8	(Garnier et al. 1997)	
<i>Bromus lanceolatus</i>	26.7	(Garnier et al. 1997)	
<i>Bromus madritensis</i>	23.6	(Garnier et al. 1997)	
<i>Bromus madritensis</i>	23.0	(Garnier et al. 1997)	
<i>Dactylis glomerata</i>	23.3	(Garnier et al. 1997)	
<i>Desmazeria rigida</i>	19.6	(Garnier et al. 1997)	
<i>Dichanthium ischaemum</i>	24.8	(Garnier et al. 1997)	
Dry alluvial meadow	30.5	(Titlyanova and Bazilevich 1979)	
Halophytic meadow–steppe	36.8	(Titlyanova and Bazilevich 1979)	
<i>Hordeum murinum</i>	16.4	(Garnier et al. 1997)	
<i>Hyparrhenia rufa</i>	16.4	(Baruch et al. 1985)	
<i>Lolium rigidum</i>	20.2	(Garnier et al. 1997)	
Matador, Canada	27.9	(Coupland and van Dyne 1979)	
Meadow–steppe	22.7	(Titlyanova and Bazilevich 1979)	
Meadow–steppe	26.9	(Titlyanova and Bazilevich 1979)	
<i>Melica ciliata</i>	18.7	(Garnier et al. 1997)	
<i>Melica ciliata</i>	18.2	(Garnier et al. 1997)	
<i>Melinis minutiflora</i>	14.6	(Baruch et al. 1985)	
Mesohalophytic meadow	23.3	(Titlyanova and Bazilevich 1979)	
Mesophytic alluvial meadow	45.5	(Titlyanova and Bazilevich 1979)	
Mesophytic alluvial meadow	25.5	(Titlyanova and Bazilevich 1979)	
Mesophytic meadow	23.6	(Titlyanova and Bazilevich 1979)	
Mesophytic meadow	21.2	(Titlyanova and Bazilevich 1979)	
<i>Panicum virgatum</i>	38.5	(Knapp 1985)	
<i>Panicum virgatum</i>	45.0	(Knapp 1985)	
<i>Phleum pratense</i>	18.7	(Garnier et al. 1997)	
Solling Plateau, Germany	17.6	(Titlyanova and Bazilevich 1979)	
Ssp. <i>Hispanica</i>	17.1	(Garnier et al. 1997)	
Steppe meadow	19.3	(Titlyanova and Bazilevich 1979)	



Grass	Mean = 25, std dev = 8.6, $n = 47$		(Continued)
Steppe meadow	21.9	(Titlyanova and Bazilevich 1979)	
Temperate grassland	27.9	(Coupland and van Dyne 1979)	
<i>Vulpia ciliata</i>	24.0	(Garnier et al. 1997)	
Shrub	Mean = 35, std dev = 12, $n = 9$		
<i>Arbutus menziesii</i>	53.3	(Field et al. 1983)	
<i>Heteromeles arbutifolia</i>	56.7	(Field et al. 1983)	
<i>Ledum palustre</i>	28.5	(Kudo 1995)	
<i>Ledum palustre</i>	30.5	(Kudo 1995)	
<i>Ledum palustre</i>	33.3	(Kudo 1995)	
<i>Prosopis glandulosa</i>	17.0	(Gausman et al. 1979)	
<i>Prunus ilicifolia</i>	32.5	(Field et al. 1983)	
<i>Rhamnus californica</i>	32.8	(Field et al. 1983)	
<i>Umbellularia californica</i>	32.2	(Field et al. 1983)	

### A.3.2 Litter carbon to nitrogen ratio

Litter carbon to nitrogen ratio ( $C:N_{lit}$ , kg C kg  $N^{-1}$ ), reflecting the leaf nitrogen content after retranslocation, is based on data from a wide number of species. Nitrogen retranslocation is 55% for ENF, 77% for DNF [calculated from  $C:N_{leaf}$  and the mean larch retranslocation rate in Gower and Richards (Gower and Richard 1990)], 55% for DBF, 45% for grass, and 53% for shrubs.

ENF	Mean = 93, std dev = 28, $n = 43$	
<i>Abies amabilis</i>	110	(Edmonds 1980)
<i>Abies amabilis</i>	110	(Ross and Tate 1993)
<i>Abies balsamea</i>	84.7	(Fyles and McGill 1987)
<i>Abies concolor</i>	68.5	(Stohlgren 1988)
<i>Abies concolor</i>	69.4	(Stohlgren 1988)
<i>Abies lasiocarpa</i>	87.3	(Stump and Binkley 1993)
<i>Abies lasiocarpa</i>	102	(Taylor et al. 1991)
<i>Calocedrus decurrens</i>	79.4	(Stohlgren 1988)
<i>Picea abies</i>	116	(Berg and McClaugherty 1989)
<i>Picea abies</i>	50.5	(Gower and Son 1992)
<i>Picea engelmannii</i>	93.8	(Stump and Binkley 1993)
<i>Picea engelmannii</i>	87.7	(Taylor et al. 1991)
<i>Picea glauca</i>	117	(Fyles and McGill 1987)
<i>Pinus banksiana</i>	103	(Fyles and McGill 1987)
<i>Pinus contorta</i>	134	(Berg and McClaugherty 1989)
<i>Pinus contorta</i>	111	(Stump and Binkley 1993)
<i>Pinus contorta</i>	135	(Fahey et al. 1985)
<i>Pinus contorta</i>	128	(Berg and Ekholm 1991)
<i>Pinus contorta</i>	49.0	(Taylor et al. 1991)
<i>Pinus elliotii</i>	143	(Gholz et al. 1985)
<i>Pinus lambertiana</i>	75.8	(Stohlgren 1988)
<i>Pinus lambertiana</i>	69.4	(Stohlgren 1988)
<i>Pinus ponderosa</i>	89.3	(Hart et al. 1992)
<i>Pinus ponderosa</i>	64.9	(Hart et al. 1992)
<i>Pinus resinosa</i>	69.4	(Gower and Son 1992)
<i>Pinus resinosa</i>	116	(Aber et al. 1990)
<i>Pinus resinosa</i>	90.9	(Pastor et al. 1984)
<i>Pinus strobus</i>	61.0	(Gower and Son 1992)

ENF	Mean = 93, std dev = 28, $n = 43$		(Continued)
<i>Pinus strobus</i>	114	(Aber et al. 1990)	
<i>Pinus strobus</i>	104	(Pastor et al. 1984)	
<i>Pinus sylvestris</i>	132	(Berg et al. 1984)	
<i>Pinus sylvestris</i>	120	(Berg and McClaugherty 1989)	
<i>Pinus sylvestris</i>	104	(Berg and Ekhhom 1991)	
<i>Pinus sylvestris</i>	132	(Staaf and Berg 1982)	
<i>Pseudotsuga menziesii</i>	100	(Aber and Melillo 1982)	
<i>Pseudotsuga menziesii</i>	49.8	(Edmonds 1980)	
<i>Pseudotsuga menziesii</i>	61.0	(Aber and Melillo 1980)	
<i>Sequoiadendron gigant.</i>	96.2	(Stohlgren 1988)	
<i>Tsuga heterophylla</i>	83.6	(Edmonds 1980)	
<i>Tsuga heterophylla</i>	60.2	(Aber et al. 1990)	
<i>Tsuga heterophylla</i>	51.0	(Pastor et al. 1984)	
DNF	Mean = 120, std dev = 24, $n = 30$		
<i>Larix decidua</i>	113	(Kloppel et al. 1998)	
<i>Larix decidua</i>	121	(Kloppel et al. 1998)	
<i>Larix decidua</i>	146	(Kloppel et al. 1998)	
<i>Larix decidua</i>	114	(Kloppel et al. 1998)	
<i>Larix decidua</i>	129	(Kloppel et al. 1998)	
<i>Larix decidua</i>	103	(Kloppel et al. 1998)	
<i>Larix decidua</i>	82.0	(Kloppel et al. 1998)	
<i>Larix decidua</i>	87.0	(Matyssek and Schulze 1987)	
<i>Larix eurolepis</i>	73.9	(Matyssek and Schulze 1987)	
<i>Larix gmelinii</i>	122	(Kloppel et al. 1998)	
<i>Larix laricina</i>	132	(Kloppel et al. 1998)	
<i>Larix laricina</i>	147	(Kloppel et al. 1998)	
<i>Larix laricina</i>	91.0	(Kloppel et al. 1998)	
<i>Larix laricina</i>	161	(Kloppel et al. 1998)	
<i>Larix leptolepis</i>	91.3	(Matyssek and Schulze 1987)	
<i>Larix lyallii</i>	96.2	(Kloppel et al. 1998)	
<i>Larix lyallii</i>	104	(Gower and Richards 1990)	
<i>Larix lyallii</i>	122	(Richards 1981)	
<i>Larix occidentalis</i>	106	(Kloppel et al. 1998)	
<i>Larix occidentalis</i>	110	(Kloppel et al. 1998)	
<i>Larix occidentalis</i>	151	(Kloppel et al. 1998)	
<i>Larix occidentalis</i>	153	(Kloppel et al. 1998)	
<i>Larix occidentalis</i>	140	(Kloppel et al. 1998)	
<i>Larix occidentalis</i>	136	(Kloppel et al. 1998)	
<i>Larix occidentalis</i>	109	(Gower 1987)	
<i>Larix occidentalis</i>	126	(Gower and Richards 1990)	
<i>Larix olgenisis</i>	142	(Kloppel et al. 1998)	
<i>Larix siberica</i>	88.0	(Kloppel et al. 1998)	
<i>Larix siberica</i>	97.0	(Kloppel et al. 1998)	
<i>Larix siberica</i>	80.8	(Kloppel et al. 1998)	
DBF	Mean = 55, std dev = 16, $n = 76$		
<i>Acer</i>	49.5	(Aber and Melillo 1980)	
<i>Acer pseudoplatanus</i>	19.8	(Bocock 1964)	
<i>Acer rubrum</i>	71.4	(Aber and Melillo 1982)	
<i>Acer rubrum</i>	75.8	(Aber et al. 1990)	
<i>Acer rubrum</i>	73.5	(Aber et al. 1990)	
<i>Acer rubrum</i>	71.4	(Melillo et al. 1982)	
<i>Acer saccharum</i>	87.8	(Gosz et al. 1973)	

DBF	Mean = 55, std dev = 16, n = 76	(Continued)
<i>Acer saccharum</i>	83.3	(Aber and Melillo 1982)
<i>Acer saccharum</i>	60.2	(Aber et al. 1990)
<i>Acer saccharum</i>	52.1	(Pastor et al. 1984)
<i>Acer saccharum</i>	83.3	(Melillo et al. 1982)
<i>Alnus glutinosa</i>	16.3	(Bocock 1964)
<i>Alnus rubra</i>	23.8	(Aber and Melillo 1982)
<i>Alnus rubra</i>	31.5	(Edmonds 1980)
<i>Alnus viridis</i>	44.1	(Fyles and McGill 1987)
<i>Betula</i>	54.3	(Aber and Melillo 1980)
<i>Betula alleghaniensis</i>	58.8	(Gosz et al. 1973)
<i>Betula Papyrifera</i>	55.6	(Aber and Melillo 1982)
<i>Betula Papyrifera</i>	55.6	(Aber et al. 1990)
<i>Betula Papyrifera</i>	55.6	(Melillo et al. 1982)
<i>Betula pendula</i>	64.9	(Berg and Ekholm 1991)
<i>Betula pubescens</i>	65.8	(Berg et al. 1984)
<i>Carya spp.</i>	38.5	(Aber and Melillo 1982)
<i>Castanea dentata</i>	47.6	(Aber and Melillo 1982)
<i>Castanea sativa</i>	114	(Cortez et al. 1996)
<i>Castanea sativa</i>	64.9	(Anderson 1973)
<i>Ceanothus spp.</i>	58.8	(Aber and Melillo 1982)
<i>Cornus florida</i>	34.4	(Aber and Melillo 1982)
<i>Corylus avellana</i>	36.0	(Bocock 1964)
<i>Fagus</i>	55.6	(Aber and Melillo 1980)
<i>Fagus grandifolia</i>	61.0	(Gosz et al. 1973)
<i>Fagus grandifolia</i>	58.8	(Aber and Melillo 1982)
<i>Fagus grandifolia</i>	55.6	(Melillo et al. 1982)
<i>Fagus sylvatica</i>	64.0	(Cortez et al. 1996)
<i>Fagus sylvatica</i>	42.7	(Bocock 1964)
<i>Fagus sylvatica</i>	42.7	(Anderson 1973)
<i>Fraxinus</i>	49.5	(Aber and Melillo 1980)
<i>Fraxinus americana</i>	55.6	(Aber and Melillo 1982)
<i>Fraxinus americana</i>	50.0	(Pastor et al. 1984)
<i>Fraxinus americana</i>	55.6	(Melillo et al. 1982)
<i>Fraxinus angustifolia</i>	53.8	(Gallardo and Merino 1993)
<i>Fraxinus excelsior</i>	33.8	(Gilbert and Bocock 1960)
<i>Fraxinus excelsior</i>	32.3	(Bocock 1964)
<i>Liriodendron tulipifera</i>	45.5	(Aber and Melillo 1982)
<i>Nothofagus spp.</i>	66.0	(Ross and Tate 1993)
<i>Populus tremuloides</i>	70.8	(Stump and Binkley 1993)
<i>Populus tremuloides</i>	60.2	(Aber et al. 1990)
<i>Prunus</i>	43.5	(Aber and Melillo 1980)
<i>Prunus avium</i>	44.6	(Bocock 1964)
<i>Prunus pennsylvanica</i>	40.0	(Aber and Melillo 1982)
<i>Prunus pennsylvanica</i>	41.7	(Melillo et al. 1982)
<i>Quercus alba</i>	62.5	(Aber and Melillo 1982)
<i>Quercus alba</i>	59.5	(Aber et al. 1990)
<i>Quercus alba</i>	56.2	(Pastor et al. 1984)
<i>Quercus canariensis</i>	71.4	(Gallardo and Merino 1993)
<i>Quercus coccinea</i>	76.9	(Aber and Melillo 1982)
<i>Quercus ilex</i>	56.5	(Cortez et al. 1996)
<i>Quercus petraea</i>	63.9	(Cortez et al. 1996)
<i>Quercus petraea</i>	68.5	(Bocock et al. 1960)
<i>Quercus petraea</i>	54.3	(Bocock 1963)

DBF	Mean = 55, std dev = 16, $n = 76$		(Continued)
<i>Quercus petraea</i>	64.9	(Bocock 1964)	
<i>Quercus petraea</i>	64.9	(Bocock 1964)	
<i>Quercus prinus</i>	41.7	(Aber and Melillo 1982)	
<i>Quercus prinus/rubra</i>	48.1	(Strojan 1978)	
<i>Quercus pyrenaica</i>	53.8	(Gallardo and Merino 1993)	
<i>Quercus robur</i>	63.3	(Bocock 1964)	
<i>Quercus rubra</i>	58.1	(Gower and Son 1992)	
<i>Quercus rubra</i>	60.2	(Aber et al. 1990)	
<i>Quercus rubra</i>	59.5	(Aber et al. 1990)	
<i>Quercus rubra</i>	61.0	(Aber et al. 1990)	
<i>Quercus rubra</i>	57.5	(Pastor et al. 1984)	
<i>Quercus suber</i>	61.7	(Gallardo and Merino 1993)	
<i>Robinia pseudoacacia</i>	32.2	(Aber and Melillo 1982)	
<i>Salix atrocinerea</i>	68.5	(Gallardo and Merino 1993)	
<i>Sassafras albidum</i>	35.2	(Strojan 1978)	
<i>Tilia americana</i>	31.2	(Pastor et al. 1984)	
Grass	Mean = 45, std dev = 11, $n = 10$		
Dry alluvial meadow	36.5	(Titlyanova and Bazilevich 1979)	
Grass	43.7	(Taylor et al. 1991)	
Halophytic meadow– steppe	51.5	(Titlyanova and Bazilevich 1979)	
Halophytic meadow	38.5	(Titlyanova and Bazilevich 1979)	
Matador, Canada	54.3	(Coupland and van Dyne 1979)	
Meadow–steppe	51.5	(Titlyanova and Bazilevich 1979)	
Meadow–steppe	35.7	(Titlyanova and Bazilevich 1979)	
Mesohalophytic meadow	37.6	(Titlyanova and Bazilevich 1979)	
Steppe–meadow	32.7	(Titlyanova and Bazilevich 1979)	
Wet halophytic meadow	69.4	(Titlyanova and Bazilevich 1979)	
Shrub	Mean = 75, std dev = 37, $n = 11$		
Alder	26.4	(Taylor et al. 1991)	
<i>Arctostaphylos</i>	66.7	(Taylor et al. 1991)	
<i>Ceanothus megacarpus</i>	74.6	(Schlessinger 1985)	
<i>Ceanothus megacarpus</i>	79.4	(Schlessinger 1985)	
<i>Cistus libanotis</i>	122	(Gallardo and Merino 1993)	
<i>Halimium halimifolium</i>	152	(Gallardo and Merino 1993)	
<i>Quercus coccifera</i>	54.9	(Gallardo and Merino 1993)	
<i>Quercus lusitanica</i>	54.9	(Gallardo and Merino 1993)	
<i>Salvia mellifera</i>	86.2	(Schlessinger 1985)	
<i>Salvia mellifera</i>	76.9	(Schlessinger 1985)	
<i>Seperdia</i>	27.9	(Taylor et al. 1991)	

### A.3.3 Fine root carbon to nitrogen ratio ( $C:N_{fr}$ , kg C kg $N^{-1}$ )

Fine root carbon to nitrogen ratio ( $C:N_{fr}$ , kg C kg  $N^{-1}$ ) controls the nitrogen required for fine root construction, but has no effect on nutrient or water uptake.

ENF	Mean = 58, std dev = 32, $n = 27$	
<i>Abies amabilis</i>	48.1	(Grier et al. 1981; Vogt et al. 1982)
<i>Abies amabilis</i>	54.9	(Grier et al. 1981; Vogt et al. 1982)
<i>Abies lasiocarpa</i>	81.5	(Stump and Binkley 1993)
ENF	59.2	(Taylor et al. 1991)
ENF	49.0	(Vogt et al. 1986)

ENF	Mean = 58, std dev = 32, $n = 27$		(Continued)
ENF	49.5	(Vogt et al. 1986)	
ENF	50.5	(Vogt et al. 1986)	
ENF	31.4	(DeAngelis et al. 1981; Nadelhoffer et al. 1985)	
ENF	36.5	(DeAngelis et al. 1981; Nadelhoffer et al. 1985)	
ENF	36.2	(DeAngelis et al. 1981; Nadelhoffer et al. 1985)	
ENF	50.0	(DeAngelis et al. 1981; Nadelhoffer et al. 1985)	
ENF	61.0	(Lutz and Cline 1947; McClaugherty et al. 1982; Vogt et al. 1986)	
ENF	40.3	(Nambiar 1987)	
ENF	42.4	(Nambiar 1987)	
<i>Picea engelmannii</i>	68.4	(Stump and Binkley 1993)	
<i>Picea/Abies</i>	27.6	(Kimmins and Hawkes 1978; Krumlik and Kimmins 1976)	
<i>Picea/Abies</i>	37.0	(Damman 1964; Damman 1971)	
<i>Picea/Abies</i>	46.7	(Damman 1964; Damman 1971)	
<i>Pinus contorta</i>	82.4	(Stump and Binkley 1993)	
<i>Pinus strobus</i>	53.6	(Aber et al. 1990)	
<i>Pinus taeda</i>	61.7	(Birk and Vitousek 1986)	
<i>Pinus taeda</i>	49.5	(Birk and Vitousek 1986)	
<i>Pinus taeda</i>	48.5	(Birk and Vitousek 1986)	
<i>Pinus taeda</i>	52.6	(Birk and Vitousek 1986)	
<i>Pinus taeda</i>	54.9	(Birk and Vitousek 1986)	
<i>Pseudotsuga menziesii</i>	79.4	(Grier et al. 1974; Santantonio et al. 1977)	
<i>Pseudotsuga menziesii</i>	200	(Grier et al. 1974; Santantonio et al. 1977)	
DNF	58	Set to ENF	
DBF	Mean = 48, std dev = 15, $n = 16$		
<i>Acer saccharum</i>	29.9	(Aber et al. 1990)	
DBF	25.0	(Fahey et al. 1978)	
DBF	53.2	(Yin 1989)	
DBF	37.6	(DeAngelis et al. 1981; Nadelhoffer et al. 1985)	
DBF	42.0	(DeAngelis et al. 1981; Nadelhoffer et al. 1985)	
DBF	43.9	(DeAngelis et al. 1981; Nadelhoffer et al. 1985)	
DBF	42.7	(DeAngelis et al. 1981; Nadelhoffer et al. 1985)	
DBF	37.9	(DeAngelis et al. 1981; Nadelhoffer et al. 1985)	
DBF	37.9	(Lutz and Cline 1947; McClaugherty et al. 1984; Vogt et al. 1986)	
DBF	58.8	(Lutz and Cline 1947; McClaugherty et al. 1984; Vogt et al. 1986)	
DBF	46.7	(Lutz and Cline 1947; McClaugherty et al. 1982; Vogt et al. 1986)	
<i>Populus tremuloides</i>	52.4	(Stump and Binkley 1993)	
<i>Quercus</i>	36.2	(Joslin and Henderson 1987)	
<i>Quercus</i>	68.5	(Joslin and Henderson 1987)	
<i>Quercus</i>	75.8	(Joslin and Henderson 1987)	
<i>Quercus</i>	73.5	(Joslin and Henderson 1987)	
Grass	Mean = 50, std dev = 19, $n = 17$		
Dry alluvial meadow	61.0	(Titlyanova and Bazilevich 1979)	
Grass	48.0	(Taylor et al. 1991)	
Halophytic meadow— Steppe	70.4	(Titlyanova and Bazilevich 1979)	
Halophytic meadow	72.5	(Titlyanova and Bazilevich 1979)	
Matador, Canada	75.8	(Coupland and van Dyne 1979)	

Grass	Mean = 50, std dev = 19, $n = 17$	(Continued)
Meadow–steppe	40.0	(Titlyanova and Bazilevich 1979)
Meadow–steppe	62.5	(Titlyanova and Bazilevich 1979)
Mesohalophytic meadow	21.7	(Titlyanova and Bazilevich 1979)
Mesohalophytic meadow	45.9	(Titlyanova and Bazilevich 1979)
Mesophytic alluvial meadow	57.5	(Titlyanova and Bazilevich 1979)
Mesophytic alluvial meadow	33.1	(Titlyanova and Bazilevich 1979)
Mesophytic meadow	42.4	(Titlyanova and Bazilevich 1979)
Solling Plateau	34.0	(Titlyanova and Bazilevich 1979)
Steppe–meadow	22.3	(Titlyanova and Bazilevich 1979)
Steppe–meadow	37.9	(Titlyanova and Bazilevich 1979)
Wet alluvial meadow	37.3	(Titlyanova and Bazilevich 1979)
Wet halophytic meadow	87.7	(Titlyanova and Bazilevich 1979)
Shrub	58	Set to ENF

### A.3.4 Live wood carbon to nitrogen ratio ( $C:N_{lw}$ , kg C kg N<sup>-1</sup>)

Limited data from small branches, which are mostly cambium, suggest that the live wood carbon to nitrogen ratio ( $C:N_{lw}$ , kg C kg N<sup>-1</sup>) is similar to  $C:N_{fr}$  (Gosz et al. 1973). Lacking data for  $C:N_{lw}$  itself, we therefore set  $C:N_{lw}$  to the mean  $C:N_{fr}$  rounded to one significant digit.

### A.3.5 Dead wood carbon to nitrogen ratio ( $C:N_{dw}$ , kg C kg N<sup>-1</sup>)

ENF	Mean = 730, std dev = 320, $n = 27$	
<i>Abies</i>	212	(Allison et al. 1963)
<i>Abies amabilis</i>	680	(Edmonds 1987)
<i>Abies concolor</i>	996	(Allison et al. 1963)
<i>Calocedrus</i>	526	(Allison et al. 1963)
<i>Cedar</i>	365	(Allison et al. 1963)
<i>Cupressus</i>	882	(Allison et al. 1963)
<i>Larix occidentalis</i>	270	(Allison et al. 1963)
<i>Picea engelmannii</i>	411	(Allison et al. 1963)
<i>Pinus contorta</i>	660	(Allison et al. 1963)
<i>Pinus contorta</i>	1400	(Fahey et al. 1985)
<i>Pinus echinata</i>	346	(Allison et al. 1963)
<i>Pinus elliotii</i>	984	(Allison et al. 1963)
<i>Pinus lambertiana</i>	404	(Allison et al. 1963)
<i>Pinus monticola</i>	433	(Allison et al. 1963)
<i>Pinus palustris</i>	1310	(Allison et al. 1963)
<i>Pinus ponderosa</i>	867	(Allison et al. 1963)
<i>Pinus strobus</i>	555	(Allison et al. 1963)
<i>Pinus strobus</i>	1250	(Berg et al. 1984)
<i>Pinus taeda</i>	716	(Allison et al. 1963)
<i>Pseudotsuga menziesii</i>	943	(Allison et al. 1963)
<i>Pseudotsuga menziesii</i>	667	(Aber and Melillo 1980)
<i>Pseudotsuga menziesii</i>	1040	(Edmonds 1987)
<i>Sequoia</i>	822	(Allison et al. 1963)
<i>Tsuga canadensis</i>	458	(Allison et al. 1963)
<i>Tsuga heterophylla</i>	991	(Edmonds 1987)
<i>Tsuga/Picea</i>	769	(Grier 1978)
Wood	710	(Harmon et al. 1986)



DNF	Set to ENF		(Continued)
DBF	Mean = 550, std dev = 121, $n = 11$		
<i>Acer</i>	556	(McClaugherty et al. 1985)	
<i>Carya</i>	468	(Allison et al. 1963)	
<i>Castanea</i>	654	(Allison et al. 1963)	
<i>Eucalyptus</i>	819	(Allison et al. 1963)	
<i>Juglans nigra</i>	470	(Allison et al. 1963)	
<i>Liriodendron tulipifera</i>	535	(Allison et al. 1963)	
<i>Quercus alba</i>	451	(Allison et al. 1963)	
<i>Quercus rubra</i>	479	(Allison et al. 1963)	
<i>Quercus stellata</i>	492	(Allison et al. 1963)	
<i>Quercus velutina</i>	676	(Allison et al. 1963)	
Wood	421	(Harmon et al. 1986)	
Grass	No woody component		
Shrub	730	Set to ENF	

A.4 Labile, cellulose, and lignin parameters

Each plant pool entering the soil decomposition subroutine is divided into three pools (two for dead wood): labile, cellulose, and lignin. The fractionation into these pools controls how rapidly decomposition occurs. In general, lab techniques are used to first measure the water and acid soluble material, which in addition to starch and sugar may include other substances, such as phenols. This is termed the labile pool. Next, cellulose is measured with an acid bath. The remainder is grouped into the lignin pool, which may include extraneous suberin (Wedin et al. 1995). Since the three pools may include different substances depending on the methodology in use, they should be considered as generalized categories, not pure labile material, cellulose, or lignin. Data sources in some cases had only one or two of the fractions listed and therefore mean biome values did not necessarily add to 100%. We first calculated lignin and cellulose fractions and let the labile percent float so that the three pools summed to 100%. For dead wood, we calculated lignin and floated cellulose.

A.4.1 Fine root fractions

For fine root fractions (percent), data sources were quite limited. Rather than set a biome value based on a single data point, we calculated the mean of all fine root data and used this for all biomes.

All biomes	Labile: mean = 34, std dev = 2.8, n = 4 Cellulose: mean = 44, std dev = 4.8, n = 6 Lignin: mean = 22, std dev = 7.3, n = 12			
	Labile	Cellulose	Lignin	
<i>Abies lasiocarpa</i>		37.8	19.8	(Stump and Binkley 1993)
<i>Acer saccharum</i>	18.5	47.7	33.8	(Taylor et al. 1991)
<i>Agropyron repens</i>			15.9	(Wedin et al. 1995)
<i>Agrostis scabra</i>			9.50	(Wedin et al. 1995)
ENF	23.3		36.1	(Taylor et al. 1991)

All biomes	Labile: mean = 34, std dev = 2.8, $n = 4$ Cellulose: mean = 44, std dev = 4.8, $n = 6$ Lignin: mean = 22, std dev = 7.3, $n = 12$			(Continued)
	Labile	Cellulose	Lignin	
Grass	22.2		24.7	(Taylor et al. 1991)
<i>Picea Engelmannii</i>		38.1	19.2	(Stump and Binkley 1993)
<i>Pinus contorta</i>		43.3	21.4	(Stump and Binkley 1993)
<i>Pinus strobus</i>	25.2	49.5	25.3	(Aber et al. 1990)
<i>Poa pratensis</i>			17.0	(Wedin et al. 1995)
<i>Populus tremuloides</i>		44.4	22.3	(Stump and Binkley 1993)
<i>Schizachyrium scopar.</i>			22.5	(Wedin et al. 1995)

### A.4.2 Litter fractions

Litter fractions (percent) were better represented in the literature and we parameterized separate biomes.

ENF	Labile: mean = 31, std dev = 12, $n = 11$ Cellulose: mean = 45, standard dev = 4.7, $n = 7$ Lignin: mean = 24, std dev = 6.7, $n = 29$			
	Labile	Cellulose	Lignin	
<i>Abies amabilis</i>			25.4	(Edmonds 1984)
<i>Abies balsamea</i>			27.6	(Fyles and McGill 1987)
<i>Abies concolor</i>			17.0	(Stohlgren 1988)
<i>Abies concolor</i>			16.2	(Stohlgren 1988)
<i>Abies lasiocarpa</i>		45.7	26.5	(Stump and Binkley 1993)
<i>Abies lasiocarpa</i>	54.4		14.6	(Taylor et al. 1991)
<i>Calocedrus decurrens</i>			9.6	(Stohlgren 1988)
<i>Picea abies</i>			34.0	(Berg and McClaugherty 1989)
<i>Picea engelmannii</i>		49.1	26.1	(Stump and Binkley 1993)
<i>Picea engelmannii</i>	48.9		14.6	(Taylor et al. 1991)
<i>Picea glauca</i>			24.9	(Fyles and McGill 1987)
<i>Pinus banksiana</i>			29.3	(Fyles and McGill 1987)
<i>Pinus contorta</i>			37.6	(Berg and McClaugherty 1989)
<i>Pinus contorta</i>		37.0	25.2	(Stump and Binkley 1993)
<i>Pinus contorta</i>	14.5		38.1	(Berg and Ekhhom 1991)
<i>Pinus contorta</i>	32.5		24.5	(Taylor et al. 1991)
<i>Pinus elliotii</i>			23.7	(Gholz et al. 1985)
<i>Pinus lambertiana</i>			18.3	(Stohlgren 1988)
<i>Pinus lambertiana</i>			16.4	(Stohlgren 1988)
<i>Pinus ponderosa</i>	18.7		26.1	(Hart et al. 1992)
<i>Pinus ponderosa</i>	21.4		30.9	(Hart et al. 1992)
<i>Pinus resinosa</i>	25.8	46.5	27.7	(Aber et al. 1990)
<i>Pinus strobus</i>	32.8	44.7	22.5	(Aber et al. 1990)
<i>Pinus sylvestris</i>	25.7	49.3	25.0	(Berg et al. 1984)
<i>Pinus sylvestris</i>			28.6	(Berg and McClaugherty 1989)
<i>Pinus sylvestris</i>	27.7		23.1	(Berg and Ekhhom 1991)
<i>Pseudotsuga menziesii</i>			24.0	(Aber and Melillo 1982)
<i>Sequoiadendron giganteum</i>			20.3	(Stohlgren 1988)
<i>Tsuga</i>	39.8	39.6	20.6	(Aber et al. 1990)
DNF	31	45	24	Set to ENF

DBF	Labile: mean = 38, std dev = 10, $n = 15$ Cellulose: mean = 44, standard dev = 11, $n = 20$ Lignin: mean = 18, std dev = 6.6, $n = 44$			(Continued)
	Labile	Cellulose	Lignin	
<i>Acer rubrum</i>			10.5	(Aber and Melillo 1982)
<i>Acer rubrum</i>	44.7	38.0	17.3	(Aber et al. 1990)
<i>Acer rubrum</i>	43.9	38.9	17.2	(Aber et al. 1990)
<i>Acer rubrum</i>			10.1	(Melillo et al. 1982)
<i>Acer saccharum</i>			10.5	(Aber and Melillo 1982)
<i>Acer saccharum</i>	44.8	43.1	12.1	(Aber et al. 1990)
<i>Acer saccharum</i>			10.1	(Melillo et al. 1982)
<i>Alnus rubra</i>			10.5	(Aber and Melillo 1982)
<i>Alnus viridis</i>			24.6	(Fyles and McGill 1987)
<i>Betula</i>	37.7	35.9	26.3	(Berg et al. 1984)
<i>Betula</i>	29.7		33.0	(Berg and Ekhhom 1991)
<i>Betula papyrifera</i>			14.0	(Aber and Melillo 1982)
<i>Betula papyrifera</i>	41.7	37.6	20.1	(Aber et al. 1990)
<i>Betula papyrifera</i>			14.5	(Melillo et al. 1982)
<i>Carya</i>			17.0	(Aber and Melillo 1982)
<i>Castanea</i>			9.0	(Aber and Melillo 1982)
<i>Castanea sativa</i>	23.4	69.4	9.2	(Cortez et al. 1996)
<i>Ceanothus</i>			10.5	(Aber and Melillo 1982)
<i>Cornus florida</i>			6.0	(Aber and Melillo 1982)
<i>Fagus</i>			23.0	(Aber and Melillo 1982)
<i>Fagus</i>			24.1	(Melillo et al. 1982)
<i>Fagus sylvatica</i>	12.4	56.1	31.5	(Cortez et al. 1996)
<i>Fraxinus</i>			12.2	(Melillo et al. 1982)
<i>Fraxinus americana</i>			12.5	(Aber and Melillo 1982)
<i>Fraxinus angustifolia</i>		29.5	10.5	(Gallardo and Merino 1993)
<i>Liriodendron tulipifera</i>			15.0	(Aber and Melillo 1982)
<i>Populus tremuloides</i>		40.6	19.4	(Stump and Binkley 1993)
<i>Populus tremuloides</i>	31.1	47.5	21.4	(Aber et al. 1990)
<i>Prunus pensylvannica</i>			18.0	(Aber and Melillo 1982)
<i>Prunus pensylvannica</i>			19.3	(Melillo et al. 1982)
<i>Quercus alba</i>			17.0	(Aber and Melillo 1982)
<i>Quercus alba</i>	32.4	47.4	20.2	(Aber et al. 1990)
<i>Quercus canariensis</i>		37.9	15.1	(Gallardo and Merino 1993)
<i>Quercus coccinea</i>			17.0	(Aber and Melillo 1982)
<i>Quercus ilex</i>	13.4	62.4	24.2	(Cortez et al. 1996)
<i>Quercus petraea</i>	21.1	56.0	24.0	(Cortez et al. 1996)
<i>Quercus prinus</i>			25.5	(Aber and Melillo 1982)
<i>Quercus pyrenaica</i>		43.1	14.3	(Gallardo and Merino 1993)
<i>Quercus rubra</i>	30.8	42.5	26.7	(Aber et al. 1990)
<i>Quercus rubra</i>	28.4	43.4	28.2	(Aber et al. 1990)
<i>Quercus rubra</i>	30.0	45.2	24.8	(Aber et al. 1990)
<i>Quercus suber</i>		42.1	18.1	(Gallardo and Merino 1993)
<i>Robinia pseudoacacia</i>			25.5	(Aber and Melillo 1982)
<i>Salix atrocinerea</i>		22.4	18.1	(Gallardo and Merino 1993)
Grass	Labile: mean = 68, std dev = NA, $n = 1$ Cellulose: mean = 23, std dev = 7.7, $n = 7$ Lignin: mean = 9.0, std dev = 4.3, $n = 13$			
	Labile	Cellulose	Lignin	
<i>Agropyron repens</i>			12.5	(Wedin et al. 1995)
<i>Agrostis scabra</i>			17.4	(Wedin et al. 1995)

Grass	Labile: mean = 68, std dev = NA, $n = 1$ Cellulose: mean = 23, std dev = 7.7, $n = 7$ Lignin: mean = 9.0, std dev = 4.3, $n = 13$			(Continued)
	Labile	Cellulose	Lignin	
<i>Dactylotaenium</i>		32.0	7.8	(Mtambanengwe and Kirchmann 1995)
Grass	30.0		12.0	(Taylor et al. 1991)
Grass pasture			12.0	(Cadisch et al. 1996)
Mixed grasses		16.2	5.3	(Singer and Harter 1996)
Mixed grasses		12.9	4.1	(Singer and Harter 1996)
Mixed grasses		17.0	5.4	(Singer and Harter 1996)
Mixed grasses		29.0	6.5	(Singer and Harter 1996)
Mixed grasses		29.6	6.1	(Singer and Harter 1996)
Mixed grasses		26.9	6.0	(Singer and Harter 1996)
<i>Poa pratensis</i>			10.7	(Wedin et al. 1995)
<i>Schizachyrium scoparium</i>			15.4	(Wedin et al. 1995)
Shrub	Labile: mean = 56, std dev = 21, $n = 7$ Cellulose: mean = 29, std dev = 8.6, $n = 4$ Lignin: mean = 15, std dev = 6.1, $n = 16$			
	Labile	Cellulose	Lignin	
<i>Alnus</i>	53.7		16.2	(Taylor et al. 1991)
Bearberry	58.1		16.6	(Taylor et al. 1991)
<i>Ceanothus megacarpus</i>	22.3		19.8	(Schlessinger 1985)
<i>Ceanothus megacarpus</i>	19.7		31.2	(Schlessinger 1985)
<i>Chilopsis linearis</i>			14.6	(Schaefer et al. 1985)
<i>Cistus libanotis</i>		17.4	8.8	(Gallardo and Merino 1993)
<i>Flourensia cernua</i>			9.6	(Schaefer et al. 1985)
<i>Halimium halimifolium</i>		26.8	8.9	(Gallardo and Merino 1993)
<i>Larrea tridentata</i>			10.6	(Schaefer et al. 1985)
<i>Prosopis glandulosa</i>			7.9	(Schaefer et al. 1985)
<i>Quercus coccifera</i>		36.4	18.8	(Gallardo and Merino 1993)
<i>Quercus lusitanica</i>		34.1	20.1	(Gallardo and Merino 1993)
<i>Salvia mellifera</i>	13.2		15.6	(Schlessinger 1985)
<i>Salvia mellifera</i>	14.3		16.9	(Schlessinger 1985)
<i>Shepherdia</i>	55.6		9.2	(Taylor et al. 1991)
<i>Yucca elata</i>			9.9	(Schaefer et al. 1985)

#### A.4.3 Dead wood fractions (percent)

ENF	Cellulose: mean = 71, std dev = 1.9, $n = 16$ Lignin: mean = 29, std dev = 3.1, $n = 19$		
	Lignin	Cellulose	
<i>Abies balsamea</i>	70.0	29.5	(Clermont and Schwartz 1951; Côte 1977; Panshin and de Zeeuw 1980; Timmell 1957)
<i>Larix laricina</i>	72.0	28.0	(Panshin and de Zeeuw 1980; Timmell 1957)
<i>Picea abies</i>	70.0	30.0	(Rydholm 1965)
<i>Picea glauca</i>	70.5	28.5	(Clermont and Schwartz 1951; Panshin and de Zeeuw 1980; Timmell 1967; Timmell 1957)
<i>Picea mariana</i>	72.5	27.5	(Clermont and Schwartz 1951; Wise and Jahn 1952)

ENF	Cellulose: mean = 71, std dev = 1.9, $n = 16$ Lignin: mean = 29, std dev = 3.1, $n = 19$		(Continued)
	Lignin	Cellulose	
<i>Pinus banksiana</i>	72.0	28.0	(Clermont and Schwartz 1951; Timmell 1957)
<i>Pinus elliotii</i>	70.0	30.0	(Panshin and de Zeeuw 1980)
<i>Pinus strobus</i>	72.5	27.5	(Clermont and Schwartz 1951; Panshin and de Zeeuw 1980; Timmell 1967)
<i>Pinus sylvestris</i>	70.0	30.0	(Rydholm 1965)
<i>Pinus Taeda</i>	71.0	29.0	(Wise and Jahn 1952)
<i>Pseudotsuga menziesii</i>	73.0	27.0	(Panshin and de Zeeuw 1980; Wise and Jahn 1952)
<i>Sequoia sempervirens</i>	66.0	34.0	(Panshin and de Zeeuw 1980)
<i>Thuja occidentalis</i>	68.0	32.0	(Côte 1977; Panshin and de Zeeuw 1980; Timmell 1957)
<i>Tsuga canadensis</i>	68.0	32.0	(Clermont and Schwartz 1951; Panshin and de Zeeuw 1980; Timmell 1967; Timmell 1957)
<i>Tsuga heterophylla</i>	70.0	30.0	(Wise and Jahn 1952)
<i>Pinus strobus</i>	68.3	22.1	(Berg et al. 1984)
<i>Pseudotsuga menziesii</i>	22.8		(Edmonds 1987)
<i>Tsuga heterophylla</i>	25.2		(Edmonds 1987)
<i>Abies amabilis</i>	32.8		(Edmonds 1987)
DNF	71	29	Set to ENF
DBF	Cellulose: mean = 77, std dev = 3.7, $n = 11$ Lignin: mean = 23, std dev = 4.9, $n = 11$		
	Lignin	Cellulose	
<i>Acer rubrum</i>	75.0	24.0	(Côte 1977; Timmell 1957)
<i>Acer rubrum</i>	80.5	12.5	(McClagherty et al. 1985)
<i>Acer saccharum</i>	75.0	25.0	(Panshin and de Zeeuw 1980)
<i>Betula lutea</i>	74.0	26.0	(Panshin and de Zeeuw 1980)
<i>Betula papyrifera</i>	81.0	19.0	(Clermont and Schwartz 1951; Timmell 1967; Timmell 1957)
<i>Betula verrucosa</i>	78.0	21.0	(Rydholm 1965)
<i>Fagus grandifolia</i>	74.0	24.0	(Panshin and de Zeeuw 1980; Timmell 1957)
<i>Populus tremuloides</i>	78.5	19.5	(Clermont and Schwartz 1951; Côte 1977; Panshin and de Zeeuw 1980; Timmell 1957)
<i>Quercus rubra</i>	75.0	25.0	(Wise and Jahn 1952)
<i>Robinea pseudoacacia</i>	68.0	32.0	(Panshin and de Zeeuw 1980)
<i>Ulmus americana</i>	74.0	24.0	(Timmell 1967)
Grass	No woody component		
Shrub	71	29	Set to ENF

## A.5 Morphological parameters

BIOME-BGC simulates the production of leaf carbon ( $\text{kg C m}^{-2} \text{ day}^{-1}$ ), which must be multiplied by specific leaf area to obtain LAI. The following parameters,

including SLA, control how leaf carbon is morphologically distributed in the leaf and canopy.

### A.5.1 Specific leaf area

LAI strongly influences all aspects of canopy physiology and is calculated as the product of SLA ( $\text{m}^2 \text{ kg C}^{-1}$ ) and leaf carbon ( $\text{kg C m}^{-2}$ ). SLA defines leaf area per unit mass: thin, light leaves, such as grass blades, have a higher SLA than dense conifer needles. SLA is also used with  $\text{C:N}_{\text{leaf}}$  to calculate leaf nitrogen content on a per unit leaf area basis. Note that the definition of SLA is in mass units of C not dry weight (as almost always reported in the literature).

ENF	Mean = 8.2, std dev = 3.6, $n = 39$	
<i>Abies grandis</i>	10.0	(Gower and Richards 1990)
<i>Juniperus virginia</i>	6.00	(Reich et al. 1995a)
<i>Picea abies</i>	7.80	(Reich et al. 1995a)
<i>Picea abies</i>	8.00	(Gower and Richards 1990)
<i>Picea abies</i>	6.80	(Bauer et al. 1997)
<i>Picea abies</i>	9.40	(Bauer et al. 1997)
<i>Picea abies</i>	9.40	(Bauer et al. 1997)
<i>Picea abies</i>	9.40	(Bauer et al. 1997)
<i>Picea abies</i>	6.40	(Bauer et al. 1997)
<i>Picea abies</i>	6.40	(Bauer et al. 1997)
<i>Picea abies</i>	6.80	(Bauer et al. 1997)
<i>Picea glauca</i>	7.00	(Reich et al. 1995a)
<i>Picea mariana</i>	7.40	(Gower and Richards 1990)
<i>Picea mariana</i>	9.76	(Kloppel et al. 1998)
<i>Picea sitchensis</i>	9.80	(Gower and Richards 1990)
<i>Pinus albicaulis</i>	10.2	(Gower and Richards 1990)
<i>Pinus albicaulis</i>	7.58	(Kloppel et al. 1998)
<i>Pinus banksiana</i>	8.20	(Reich et al. 1995a)
<i>Pinus contorta</i>	8.00	(Gower 1987)
<i>Pinus contorta</i>	7.60	(Gower and Richards 1990)
<i>Pinus contorta</i>	9.76	(Kloppel et al. 1998)
<i>Pinus ponderosa</i>	2.40	(Cregg 1994)
<i>Pinus ponderosa</i>	2.08	(Cregg 1994)
<i>Pinus ponderosa</i>	2.01	(Cregg 1994)
<i>Pinus ponderosa</i>	2.44	(Cregg 1994)
<i>Pinus ponderosa</i>	2.25	(Cregg 1994)
<i>Pinus resinosa</i>	8.00	(Reich et al. 1995a)
<i>Pinus resinosa</i>	5.60	(Reich et al. 1995a)
<i>Pinus resinosa</i>	10.0	(Gower and Richards 1990)
<i>Pinus strobus</i>	11.4	(Reich et al. 1995a)
<i>Pinus strobus</i>	14.8	(Reich et al. 1995a)
<i>Pinus strobus</i>	14.8	(Gower and Richards 1990)
<i>Pinus sylvestris</i>	6.80	(Reich et al. 1995a)
<i>Pseudotsuga menziesii</i>	9.00	(Gower 1987)
<i>Pseudotsuga menziesii</i>	8.74	(Kloppel et al. 1998)
<i>Pseudotsuga menziesii</i>	8.76	(Kloppel et al. 1998)
<i>Thuja occidentalis</i>	9.00	(Reich et al. 1995a)
<i>Tsuga heterophylla</i>	21.0	(Gower and Richards 1990)
<i>Tsuga mertensiana</i>	9.20	(Gower and Richards 1990)



DNF	Mean = 22, std dev = 4.2, n = 15		(Continued)
<i>Larix decidua</i>	24.6	(Gower and Richards 1990)	
<i>Larix decidua</i>	16.0	(Matyssek and Schulze 1987)	
<i>Larix eurolepis</i>	17.9	(Matyssek and Schulze 1987)	
<i>Larix laricina</i>	23.2	(Gower and Richards 1990)	
<i>Larix laricina</i>	24.8	(Kloeppel et al. 1998)	
<i>Larix leptolepis</i>	28.2	(Gower and Richards 1990)	
<i>Larix leptolepis</i>	18.8	(Matyssek and Schulze 1987)	
<i>Larix lyallii</i>	26.4	(Gower and Richards 1990)	
<i>Larix lyallii</i>	21.2	(Richards 1981)	
<i>Larix occidentalis</i>	16.8	(Gower 1987)	
<i>Larix occidentalis</i>	15.2	(Gower and Richards 1990)	
<i>Larix occidentalis</i>	26.4	(Kloeppel et al. 1998)	
<i>Larix occidentalis</i>	22.8	(Kloeppel et al. 1998)	
<i>Larix occidentalis</i>	24.0	(Kloeppel et al. 1998)	
<i>Larix occidentalis</i>	25.6	(Kloeppel et al. 1998)	
DBF	Mean = 32, std dev = 11, n = 96		
<i>Acer negundo</i>	44.4	(Abrams et al. 1994)	
<i>Acer rubrum</i>	33.2	(Reich et al. 1995a)	
<i>Acer rubrum</i>	46.6	(Reich et al. 1995a)	
<i>Acer saccharum</i>	26.6	(Reich et al. 1995a)	
<i>Acer saccharum</i>	23.6	(Reich et al. 1995a)	
<i>Acer saccharum</i>	52.6	(Abrams et al. 1994)	
<i>Acer saccharum</i>	36.6	(Burton et al. 1991)	
<i>Acer saccharum</i>	44.0	(Burton et al. 1991)	
<i>Acer saccharum</i>	35.4	(Burton et al. 1991)	
<i>Acer saccharum</i>	34.4	(Burton et al. 1991)	
<i>Acer saccharum</i>	42.8	(Burton et al. 1991)	
<i>Acer saccharum</i>	31.1	(Jose and Gillespie 1996)	
<i>Betula lenta</i>	44.4	(Abrams et al. 1994)	
<i>Betula nigra</i>	23.6	(Reich et al. 1995a)	
<i>Betula pendula</i>	33.3	(Kull and Niinemets 1993)	
<i>Betula pumila</i>	19.6	(Reich et al. 1995a)	
<i>Beureria cumanensis</i>	23.3	(Holbrook et al. 1995)	
<i>Bulnesia arborea</i>	22.0	(Holbrook et al. 1995)	
<i>Carya cordiformis</i>	50.0	(Abrams et al. 1994)	
<i>Carya glabra</i>	26.9	(Jose and Gillespie 1996)	
<i>Carya ovata</i>	22.4	(Reich et al. 1995a)	
<i>Castanea dentata</i>	34.5	(Abrams et al. 1994)	
<i>Celtis occidentalis</i>	24.2	(Reich et al. 1995a)	
<i>Celtis tenuifolia</i>	23.5	(Abrams et al. 1994)	
<i>Coccoloba liebmanni</i>	25.0	(Holbrook et al. 1995)	
<i>Cochlospermum vitifolium</i>	37.0	(Holbrook et al. 1995)	
<i>Cornus alternifolia</i>	26.7	(Abrams et al. 1994)	
<i>Cornus florida</i>	21.6	(Reich et al. 1995a)	
<i>Fagus grandifolia</i>	29.3	(Jose and Gillespie 1996)	
<i>Fagus sylvatica</i>	27.8	(Bauer et al. 1997)	
<i>Fagus sylvatica</i>	48.0	(Bauer et al. 1997)	
<i>Fagus sylvatica</i>	37.0	(Bauer et al. 1997)	
<i>Fagus sylvatica</i>	37.8	(Bauer et al. 1997)	
<i>Fagus sylvatica</i>	38.8	(Bauer et al. 1997)	
<i>Forchhammeria pallida</i>	28.6	(Holbrook et al. 1995)	
<i>Fraxinus americana</i>	26.4	(Reich et al. 1995a)	

DBF	Mean = 32, std dev = 11, n = 96	(Continued)
<i>Fraxinus americana</i>	27.6	(Reich et al. 1995a)
<i>Fraxinus americana</i>	30.8	(Abrams et al. 1994)
<i>Fraxinus nigra</i>	52.6	(Abrams et al. 1994)
<i>Genipa caruto</i>	20.8	(Holbrook et al. 1995)
<i>Godmania macrocarpa</i>	16.3	(Holbrook et al. 1995)
<i>Humboldtella arborea</i>	54.1	(Holbrook et al. 1995)
<i>Ilex verticillata</i>	24.4	(Reich et al. 1995a)
<i>Jacquinia pungens</i>	20.0	(Holbrook et al. 1995)
<i>Juglans nigra</i>	61.0	(Reich et al. 1995a)
<i>Juglans nigra</i>	30.8	(Abrams et al. 1994)
<i>Liriodendron tulipifera</i>	20.5	(Jose and Gillespie 1996)
<i>Lonchocarpus dipteroneurus</i>	48.8	(Holbrook et al. 1995)
<i>Lonicera x bella</i>	21.8	(Reich et al. 1995a)
<i>Luehea candida</i>	46.5	(Holbrook et al. 1995)
<i>Mansoa verrucifera</i>	35.1	(Holbrook et al. 1995)
<i>Morus rubra</i>	36.4	(Reich et al. 1995a)
<i>Pereskia guamacho</i>	37.0	(Holbrook et al. 1995)
<i>Pithecellobium carabobense</i>	23.5	(Holbrook et al. 1995)
<i>Pithecellobium dulce</i>	30.3	(Holbrook et al. 1995)
<i>Pithecellobium ligustrinum</i>	30.8	(Holbrook et al. 1995)
<i>Populus deltoides</i>	21.8	(Reich et al. 1995a)
<i>Populus hybrid</i>	24.8	(Heilman and Fu-Guang 1994)
<i>Populus hybrid</i>	25.2	(Heilman and Fu-Guang 1994)
<i>Populus hybrid</i>	22.4	(Heilman and Fu-Guang 1994)
<i>Populus hybrid</i>	26.6	(Heilman and Fu-Guang 1994)
<i>Populus hybrid</i>	24.4	(Heilman and Fu-Guang 1994)
<i>Populus hybrid</i>	21.4	(Heilman and Fu-Guang 1994)
<i>Populus hybrid</i>	32.0	(Heilman and Fu-Guang 1994)
<i>Populus hybrid</i>	29.0	(Heilman and Fu-Guang 1994)
<i>Populus hybrid</i>	27.4	(Heilman and Fu-Guang 1994)
<i>Populus hybrid</i>	29.2	(Heilman and Fu-Guang 1994)
<i>Populus hybrid</i>	30.0	(Heilman and Fu-Guang 1994)
<i>Populus hybrid</i>	23.4	(Heilman and Fu-Guang 1994)
<i>Populus tremuloides</i>	24.2	(Reich et al. 1995a)
<i>Prunus pensylvanica</i>	30.8	(Abrams et al. 1994)
<i>Prunus serotina</i>	19.8	(Reich et al. 1995a)
<i>Prunus serotina</i>	50.0	(Reich et al. 1995a)
<i>Prunus serotina</i>	40.0	(Abrams et al. 1994)
<i>Prunus serotina</i>	26.7	(Jose and Gillespie 1996)
<i>Quercus alba</i>	20.4	(Jose and Gillespie 1996)
<i>Quercus ellipsoidalis</i>	19.0	(Reich et al. 1995a)
<i>Quercus ellipsoidalis</i>	37.0	(Reich et al. 1995a)
<i>Quercus macrocarpa</i>	22.8	(Reich et al. 1995a)
<i>Quercus macrocarpa</i>	33.3	(Abrams et al. 1994)
<i>Quercus prinus</i>	19.9	(Jose and Gillespie 1996)
<i>Quercus rubra</i>	26.2	(Reich et al. 1995a)
<i>Quercus rubra</i>	27.0	(Reich et al. 1995a)
<i>Quercus rubra</i>	20.2	(Jose and Gillespie 1996)
<i>Quercus velutina</i>	25.0	(Abrams et al. 1994)
<i>Randia aculeata</i>	60.6	(Holbrook et al. 1995)
<i>Rhamnus cathartica</i>	22.0	(Reich et al. 1995a)
<i>Rubus allighaniensis</i>	54.0	(Reich et al. 1995a)
<i>Salix dasyclados</i>	27.2	(Kull et al. 1998)

DBF	Mean = 32, std dev = 11, n = 96		(Continued)
<i>Salix viminalis</i>	30.1	(Kull et al. 1998)	
<i>Sassafras albidum</i>	30.8	(Abrams et al. 1994)	
<i>Tabebuia billergiana</i>	38.5	(Holbrook et al. 1995)	
<i>Tillia americana</i>	66.7	(Abrams et al. 1994)	
Tropical deciduous forest	36.4	(Maass et al. 1995)	
<i>Ulmus americana</i>	16.8	(Reich et al. 1995a)	
<i>Ulmus rubra</i>	22.2	(Abrams et al. 1994)	
Grass	Mean = 49, std dev = 16, n = 35		
<i>Aegilops ovata</i>	46.2	(Garnier et al. 1997)	
<i>Agropyron sp.</i>	55.0	(Garnier et al. 1997)	
<i>Andropogon gerardii</i>	32.8	(Knapp 1985)	
<i>Andropogon gerardii</i>	41.5	(Knapp 1985)	
<i>Avena barbata</i>	50.8	(Garnier et al. 1997)	
<i>Avenula bromoides</i>	36.8	(Garnier et al. 1997)	
<i>Brachypodium distachyon</i>	65.6	(Garnier et al. 1997)	
<i>Brachypodium phoenicoides</i>	31.4	(Garnier et al. 1997)	
<i>Brachypodium phoenicoides</i>	33.2	(Garnier et al. 1997)	
<i>Brachypodium retusum</i>	35.4	(Garnier et al. 1997)	
<i>Brachypodium retusum</i>	36.8	(Garnier et al. 1997)	
<i>Bromus erectus</i>	34.0	(Garnier et al. 1997)	
<i>Bromus erectus</i>	40.4	(Garnier et al. 1997)	
<i>Bromus erectus</i>	44.0	(Garnier et al. 1997)	
<i>Bromus hordeaceus</i>	56.4	(Garnier et al. 1997)	
<i>Bromus lanceolatus</i>	57.6	(Garnier et al. 1997)	
<i>Bromus madritensis</i>	74.0	(Garnier et al. 1997)	
<i>Bromus madritensis</i>	71.6	(Garnier et al. 1997)	
<i>Dactylis glomerata</i>	40.8	(Garnier et al. 1997)	
<i>Dactylis glomerata</i>	43.6	(Garnier et al. 1997)	
<i>Desmazeria rigida</i>	46.6	(Garnier et al. 1997)	
<i>Dichantium ischaemum</i>	58.0	(Garnier et al. 1997)	
Grass	15.8	(McWilliam et al. 1993)	
<i>Hordeum murinum</i>	58.8	(Garnier et al. 1997)	
<i>Lolium rigidum</i>	50.6	(Garnier et al. 1997)	
<i>Melica ciliata</i>	49.8	(Garnier et al. 1997)	
<i>Melica ciliata</i>	43.0	(Garnier et al. 1997)	
<i>Panicum virgatum</i>	37.1	(Knapp 1985)	
<i>Panicum virgatum</i>	39.0	(Knapp 1985)	
<i>Paspalum dilatatum</i>	66.0	(Clark et al. 1997)	
<i>Phleum pratense</i>	54.2	(Garnier et al. 1997)	
<i>Trifolium repens</i>	50.0	(Clark et al. 1997)	
<i>Trifolium repens</i>	68.0	(Clark et al. 1997)	
<i>Trifolium repens</i>	88.0	(Clark et al. 1997)	
<i>Vulpia ciliata</i>	75.4	(Garnier et al. 1997)	
Shrub	Mean = 12, std dev = 5.1, n = 9		
<i>Gaultheria antipoda</i>	17.6	(Körner et al. 1986)	
<i>Gaultheria antipoda</i>	18.1	(Körner et al. 1986)	
<i>Gaultheria depressa</i>	14.7	(Körner et al. 1986)	
<i>Gaultheria depressa</i>	14.6	(Körner et al. 1986)	
<i>Ledum palustre</i>	5.62	(Kudo 1995)	
<i>Ledum palustre</i>	11.4	(Kudo 1995)	
<i>Ledum palustre</i>	13.4	(Kudo 1995)	
<i>Pernettya alpina</i>	13.6	(Körner et al. 1986)	
<i>Retama sphaerocarpa</i>	3.00	(Pugnaire et al. 1996)	

### A.5.2 All-sided to projected leaf area index ratio

Most canopy processes are estimated on a projected leaf area basis (the leaf area projected horizontally on the ground surface). Canopy water interception, though, is calculated under the assumption that all leaf surfaces retain water. Projected LAI therefore must be converted to all-sided LAI with  $\text{LAI}_{\text{all:proj}}$  ( $\text{LAI LAI}^{-1}$ ). For flat leaves (grass and DBF)  $\text{LAI}_{\text{all:proj}}$  is 2.0 and is not referenced. Needles are not flat and all-sided leaf area is greater. Accurate measurement of  $\text{LAI}_{\text{all:proj}}$  can be made by microscopic analysis of needle cross-sectional perimeter divided by maximum width (Cregg 1994) or by geometric approximations (Fassnacht et al. 1994). The mean value of 2.6 agrees with the general conifer value reported by Körner (Körner 1995). We assumed that shrub leaves were intermediate in shape and set shrub  $\text{LAI}_{\text{all:proj}}$  to 2.3.

ENF		Mean = 2.6, std dev = 0.29, $n = 11$
<i>Pinus ponderosa</i>	2.45	(Cregg 1994)
<i>Pinus ponderosa</i>	2.40	(Cregg 1994)
<i>Pinus ponderosa</i>	2.37	(Cregg 1994)
<i>Pinus ponderosa</i>	2.37	(Cregg 1994)
<i>Pinus ponderosa</i>	2.44	(Cregg 1994)
<i>Pinus contorta</i>	2.57	(Barclay 1998)
<i>Pinus strobus</i>	2.54	(Swank and Schreuder 1973)
<i>Pinus</i>	3.14	(Deblonde et al. 1994)
<i>Pinus</i>	3.14	(Fassnacht et al. 1994)
<i>Pinus</i>	2.57	(Fassnacht et al. 1994)
<i>Pinus</i>	2.30	(Drew and Running 1975)
DNF	2.6	Set to ENF
DBF		
	Defined as 2.0	
Grass		
	Defined as 2.0	
Shrub		
	2.3	See text for discussion

### A.5.3 Shaded to sunlit specific leaf area ratio

Nonlinear physiological responses to absorbed radiation tend to produce significant errors in predicted carbon and water fluxes in big leaf models (de Pury and Farquhar 1997) such as the original FOREST-BGC (Running and Coughlan 1988; Running and Gower 1991). Simulating multiple canopy layers obviates this problem, but is complicated and computationally expensive. De Pury and Farquhar (de Pury and Farquhar 1997) found that a two-layer model with sunlit and shaded portions solves most of the big leaf problems without excessive complexity and Thornton (Thornton 1998) describes the implementation of this approach in BIOME-BGC. Essentially, leaf nitrogen on a mass basis tends to stay relatively constant with canopy depth (Ellsworth and Reich 1993), but SLA increases, necessitating different SLAs for sunlit and shaded canopy fractions. Poorter and Evans (Poorter and Evans 1998) found that for a variety of shrub, tree, and herbaceous species, SLA in low irradiance was approximately twice the SLA in high irradiance while mass-based Rubisco content was essentially constant. We assigned 2.0 for  $\text{SLA}_{\text{shd:sun}}$  ( $\text{SLA SLA}^{-1}$ ) for all biomes.

## A.6 Conductance rates and limitations

Leaf gas exchange is modeled through an electrical circuit analogy (Nobel 1991) with stomatal and cuticular conductance in parallel and leaf boundary layer conductance in series. The parameters controlling leaf conductance are important for regulating water loss and carbon assimilation. In this section, we consider the parameterization of maximum stomatal conductance, cuticular conductance, boundary layer conductance, and the two main parameters limiting stomatal aperture: leaf water potential and vapor pressure deficit.

### A.6.1 Maximum stomatal conductance

Maximum stomatal conductance ( $g_{\text{max}}$ ,  $\text{m s}^{-1}$ ) establishes the rate of conductance ( $g$ ) when environmental conditions are nonlimiting. Major differences do exist between agricultural and natural vegetation, but within natural vegetation types, the major functional types are remarkably similar. Three reviews (Kelliher et al. 1995; Körner 1995; Schulze et al. 1994) all reached the same conclusion:  $g_{\text{max}}$  does not vary significantly between natural vegetation types. There is some discussion that grasslands may have higher  $g_{\text{max}}$  (Körner 1995), but to date there is insufficient evidence to establish this position. Thus, overwhelming evidence in this case led us to assign a single value for each biome. We adopted the most recent estimate, from Kelliher et al. (Kelliher et al. 1995), of  $0.006 \text{ m s}^{-1}$  for all biomes.

### A.6.2 Cuticular conductance

Even when stomata are completely closed, gas exchange will still take place at very low rates through cuticular conductance ( $g_{\text{cut}}$ ,  $\text{m s}^{-1}$ ). Essentially, leaf cuticles are somewhat leaky to gas exchange. Unfortunately, accurate measurements of  $g_{\text{cut}}$  are rare and often inaccurate (Körner 1995). Measurement of  $g_{\text{cut}}$  in the field is limited because plants almost never reach complete stomatal closure. Laboratory measurements of  $g_{\text{cut}}$  almost always obtain lower values than  $g_{\text{cut}}$  in the field. Measurements of  $g_{\text{cut}}$  relevant for BIOME-BGC, at which stomata are completely closed, are almost impossible to obtain in the field. We therefore applied the lowest level reported by Körner (Körner 1995) of 1/100th of  $g_{\text{max}}$ , or  $0.00006 \text{ m s}^{-1}$ .

### A.6.3 Boundary layer conductance

Boundary layer conductance ( $g_{\text{bl}}$ ,  $\text{m s}^{-1}$ ) controls gas diffusion through the stable boundary layer around the leaf surface ( $\delta_{\text{bl}}$ ). Increases in leaf length in the wind direction increase  $\delta_{\text{bl}}$  according to a power function; increases in wind speed exponentially decrease  $\delta_{\text{bl}}$ . Wind speed is not prescribed in BIOME-BGC and we assumed  $0.45 \text{ m s}^{-1}$ . Fitting a curve to data in Nobel (Nobel 1991),  $\delta_{\text{bl}} = 5.9574 L^{0.4982}$ , where  $\delta_{\text{bl}}$  is leaf boundary layer thickness (mm) and  $L$  is leaf length in the wind direction (m). For BIOME-BGC,  $L=0.002 \text{ m}$  and  $\delta_{\text{bl}}=0.27 \text{ mm}$  (needle leaf),  $L=0.08 \text{ m}$  and  $\delta_{\text{bl}}=1.7$  (broad leaf),  $L=0.01 \text{ m}$  and  $\delta_{\text{bl}}=0.60 \text{ mm}$  (grass), and  $L=0.04 \text{ m}$  and  $\delta_{\text{bl}}=1.2 \text{ mm}$  (shrub). Following Nobel (Nobel 1991) boundary layer conductance is  $g_{\text{bl}} = D_{\text{wv}}/\delta_{\text{bl}}$ , where  $D_{\text{wv}}$  is the diffusion coefficient of water vapor in air ( $2.4 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$  at  $0.103 \text{ MPa}$  and  $20^\circ\text{C}$ ). Calculated values were  $0.09$  (ENF and DNF),  $0.01$  (DBF),  $0.04$  (grass), and  $0.02$  (shrub).

### A.6.4 Leaf water potential at initial and final reduction to stomatal conductance

Plant water stress, as measured in negative leaf water potential ( $\Psi_l$ ), is a commonly observed cause of stomatal closure. As leaf water potential drops below critical levels, leaf desiccation occurs, guard cell turgor is lost, and stomatal closure occurs. Diurnal plots can show a strong correlation between  $g$  and  $\Psi_l$  (Carlson et al. 1979). However, as seen in cases where maximal  $g$  occurs at minimal  $\Psi_l$  (Gallego et al. 1994; Hacke and Sauter 1995; Koch et al. 1994), there is no unique relationship between  $\Psi_l$  and  $g$ . Other factors, such as vapor pressure deficit (VPD), directly influence the diurnal values of  $\Psi_l$ . Diurnal plots of  $\Psi_l$  versus  $g$  are therefore not useful for the parameterization. As shown by (Running 1976), the predawn leaf water potential ( $\Psi_{lpd}$ ) is highly correlated with  $g_{smax}$ . In this case, the plant is responding to long-term changes in soil water potential ( $\Psi_s$ ), not daily variation in  $\Psi_l$ . Given no transpiration during the night,  $\Psi_{lpd}$  is usually approximately equal to  $\Psi_s$  (Kozlowski et al. 1991). Thus,  $\Psi_{lpd}$  acts as a surrogate measure for  $\Psi_s$ .

We calculated two parameters: the  $\Psi_{lpd}$  at which initial reduction to stomatal conductance occurs ( $\Psi_i$ ) and the  $\Psi_{lpd}$  at which final reduction to stomatal conductance occurs ( $\Psi_f$ ), that is, complete stomatal closure. In most cases,  $\Psi_i$  and  $\Psi_f$  were not reported and we subjectively extracted parameter values from scatterplots.

ENF	Initial: mean = $-0.65$ , std dev = $0.23$ , $n = 15$ Final: mean = $-2.5$ , std dev = $1.0$ , $n = 15$		
	Initial	Final	
<i>Abies bornmulleriana</i>	$-0.20$	$-2.0$	(Guehl 1991)
<i>Cedrus atlantica</i>	$-0.50$	$-3.3$	(Guehl 1991)
<i>Juniperus monosperma</i>	$-0.50$	$-2.8$	(Lajtha and Barnes 1991)
<i>Juniperus osteosperma</i>	$-1.0$	$-3.0$	(DeLucia and Schlesinger 1990)
<i>Picea glauca</i>	$-0.50$	$-1.5$	(Eastman and Camm 1995)
<i>Picea glauca</i>	$-0.60$	$-1.8$	(Goldstein et al. 1985)
<i>Picea mariana</i>	$-0.50$	$-4.0$	(Dang et al. 1997)
<i>Pinus banksiana</i>	$-1.0$	$-2.8$	(Dang et al. 1997)
<i>Pinus contorta</i>	$-0.50$	$-1.4$	(Running 1980)
<i>Pinus edulis</i>	$-1.0$	$-5.0$	(Lajtha and Barnes 1991)
<i>Pinus jeffreyi</i>	$-0.70$	$-2.0$	(DeLucia and Schlesinger 1990)
<i>Pinus monophylla</i>	$-0.70$	$-2.0$	(DeLucia and Schlesinger 1990)
<i>Pinus ponderosa</i>	$-0.80$	$-1.5$	(Cregg 1994)
<i>Pinus ponderosa</i>	$-0.50$	$-2.2$	(DeLucia et al. 1988)
<i>Pinus ponderosa</i>	$-0.70$	$-2.0$	(DeLucia and Schlesinger 1990)
DNF	$-0.65$	$-2.5$	Set to ENF
DBF	Initial: mean = $-0.34$ , std dev = $0.14$ , $n = 11$ Final: mean = $-2.2$ , std dev = $0.70$ , $n = 11$		
	Initial	Final	
<i>Acer saccharum</i>	$-0.20$	$-1.3$	(Ni and Pallardy 1991)
<i>Juglans nigra</i>	$-0.20$	$-1.5$	(Ni and Pallardy 1991)
<i>Quercus afares</i>	$-0.50$	$-2.0$	(Acherar and Rambal 1992)
<i>Quercus alba</i>	$-0.20$	$-2.0$	(Ni and Pallardy 1991)
<i>Quercus faginea</i>	$-0.50$	$-2.0$	(Acherar and Rambal 1992)



DBF	Initial: mean = $-0.34$ , std dev = $0.14$ , $n = 11$ Final: mean = $-2.2$ , std dev = $0.70$ , $n = 11$		(Continued)
	Initial	Final	
<i>Quercus marilandica</i>	$-0.50$	$-3.5$	(Reich and Hinckley 1980)
<i>Quercus petraea</i>	$-0.30$	$-3.0$	(Epron and Dreyer 1993)
<i>Quercus petraea</i>	$-0.30$	$-2.5$	(Bréda et al. 1993)
<i>Quercus pubescens</i>	$-0.50$	$-3.0$	(Dameisin and Rambal 1995)
<i>Quercus rubra</i>	$-0.30$	$-2.2$	(Crunkilton et al. 1992)
<i>Quercus stellata</i>	$-0.20$	$-1.5$	(Ni and Pallardy 1991)
Grass	Initial: mean = $-0.73$ , std dev = $0.71$ , $n = 4$ Final: mean = $-2.7$ , std dev = $1.2$ , $n = 4$		
	Initial	Final	
<i>Leersia hexandra</i>	$-1.7$	$-3.3$	(Kirkman and Sharitz 1993)
<i>Manisuris rugosa</i>	$-0.20$	$-1.3$	(Kirkman and Sharitz 1993)
<i>Panicum hemitomon</i>	$-0.80$	$-2.3$	(Kirkman and Sharitz 1993)
<i>Poa sand bergii</i>	$-0.20$	$-4.0$	(Link et al. 1990)
Shrub	Initial: mean = $-0.81$ , std dev = $0.27$ , $n = 10$ Final: mean = $-4.2$ , std dev = $1.6$ , $n = 10$		
	Initial	Final	
<i>Artemesia tridentata</i>	$-0.50$	$-5.0$	(DeLucia et al. 1988)
<i>Artemesia tridentata</i>	$-0.80$	$-4.0$	(S. D. Smith et al. 1997)
<i>Artemesia tridentata</i>	$-1.0$	$-3.5$	(S. D. Smith et al. 1997)
<i>Ceanothus thyrsiflorus</i>	$-0.30$	$-2.5$	(Tenhunen et al. 1994)
<i>Colegyne ramosissima</i>	$-1.0$	$-7.0$	(Smith et al. 1995)
<i>Ephedra nevadensis</i>	$-1.0$	$-5.0$	(Smith et al. 1995)
<i>Eucalyptus socialis</i>	$-1.0$	$-3.0$	(Collatz et al. 1976)
<i>Haplopappus cooperi</i>	$-1.0$	$-6.0$	(Smith et al. 1995)
<i>Larrea tridentata</i>	$-1.0$	$-4.5$	(Franco et al. 1994)
<i>Nerium oleander</i>	$-0.50$	$-1.8$	(Gollan et al. 1985)

### A.6.5 Vapor pressure deficit at initial and final reduction to stomatal conductance

High leaf to atmosphere VPD is commonly observed to cause reductions in stomatal conductance. The precise mechanism, probably either a stomatal response to transpiration-induced reduction in guard cell water potential (feedback response) or a direct stomatal sensitivity to increased VPD independent of leaf water status (feedforward response), is not completely understood. Evidence exists for both the feedforward (Schulze et al. 1972) and feedback (Monteith 1995) mechanisms with some authors finding intermediate response mechanisms (Franks et al. 1997).

We collected VPD versus  $g$  data for the five functional types. To do so, we extracted two values from the literature: the VPD at initial stomatal closure ( $VPD_i$ ) and the VPD at final stomatal closure ( $VPD_f$ ). As for  $\Psi$ , these data are usually presented in a scatterplot format. Therefore, parameter extraction was again subjective. We assumed that responses were linear (Körner 1995) and extrapolated from the presented data to a value of zero  $g$ . In cases where multiple response functions were shown, we used data in which other conditions (radiation, temperature, soil water, etc.) were least limiting and for the initial exposure to drought.

ENF	Initial: mean = 0.61, std dev = 0.17, $n = 10$ Final: mean = 3.1, std dev = 1.4, $n = 10$		
	Initial	Final	
<i>Abies alba</i>	0.50	2.0	(Guehl 1991)
<i>Abies cephalonica</i>	0.50	2.0	(Guehl 1991)
<i>Abies marocana</i>	0.50	2.0	(Guehl 1991)
<i>Abies nordmanniana</i>	0.50	2.0	(Guehl 1991)
<i>Juniperus occidentalis</i>	1.0	5.0	(Miller et al. 1993)
<i>Picea glauca</i>	0.50	2.5	(Goldstein et al. 1985)
<i>Picea mariana</i>	0.50	6.0	(Dang et al. 1997)
<i>Pinus banksiana</i>	0.80	3.8	(Dang et al. 1997)
<i>Pinus sylvestris</i>	0.60	2.5	(Kellomäki and Wang 1997)
<i>Pseudotsuga menziesii</i>	0.70	3.5	(Meinzer 1982)
DNF	0.61	3.1	Set to ENF
DBF	Initial: mean = 1.1, std dev = 0.53, $n = 7$ Final: mean = 3.6, std dev = 0.80, $n = 7$		
	Initial	Final	
<i>Acer saccharum</i>	1.2	3.4	(Ellsworth and Reich 1992b)
<i>Betula pendula</i>	1.0	4.0	(Osonubi and Davies 1980)
<i>Fagus sylvatica</i>	0.60	3.0	(Kersteins 1995)
<i>Populus angustifolia</i>	2.0	4.7	(Foster and Smith 1991)
<i>Populus nigra</i>	0.50	3.5	(Appleby and Davies 1983)
<i>Populus tremuloides</i>	1.0	4.2	(Dang et al. 1997)
<i>Ulmus glabra</i>	1.6	2.3	(Appleby and Davies 1983)
Grass	Initial: mean = 1.0, std dev = 0.25, $n = 11$ Final: mean = 5.0, std dev = 2.7, $n = 11$		
	Initial	Final	
<i>Abutilon theophrasti</i>	1.0	2.0	(Bunce 1996)
<i>Amaranthus hypochondriacus</i>	0.70	3.0	(Bunce 1993)
<i>Ambrosia chamissonis</i>	0.80	3.0	(Mooney and Chu 1983)
<i>Eriogonum latifolium</i>	1.0	3.5	(Mooney and Chu 1983)
<i>Fragaria chiloensis</i>	1.0	3.5	(Mooney and Chu 1983)
<i>Heteropogon contortis</i>	1.5	6.0	(Williams and Black 1994)
<i>Hyparrhenia rufa</i>	1.0	5.5	(Baruch et al. 1985)
<i>Leymus cinereus</i>	1.2	5.0	(S. D. Smith et al. 1997)
<i>Melinis minutifolia</i>	1.0	5.5	(Baruch et al. 1985)
<i>Pennisetum setaceum</i>	1.5	12	(Williams and Black 1994)
<i>Trachypogon plumosus</i>	1.0	6.0	(Baruch et al. 1985)
Shrub	Initial: mean = 0.97, std dev = 0.24, $n = 9$ Final: mean = 4.1, std dev = 1.0, $n = 9$		
	Initial	Final	
<i>Arbutus unedo</i>	1.0	4.0	(Tenhunen et al. 1982)
<i>Arbutus unedo</i>	1.0	3.5	(Turner et al. 1985)
<i>Artemesia tridentata</i>	0.80	5.0	(S. D. Smith et al. 1997)
<i>Artemesia tridentata</i>	0.80	6.0	(S. D. Smith et al. 1997)
<i>Larrea tridentata</i>	1.0	3.3	(Franco et al. 1994)
<i>Nerium oleander</i>	1.0	5.0	(Gollan et al. 1985)
<i>Nerium oleander</i>	1.5	4.0	(Turner et al. 1985)
<i>Psychotria horizontalis</i>	0.60	2.5	(Hogan et al. 1994)
<i>Yucca glauca</i>	1.0	4.0	(Roessler and Monson 1985)

## A.7 Miscellaneous parameters

### A.7.1 Water interception coefficient

The water interception coefficient ( $W_{\text{int}}$ ,  $1 \text{ LAI}^{-1} \text{ day}^{-1}$ ) determines the amount of precipitation intercepted by the canopy. Canopy interception in turn controls the amount of precipitation entering the soil water pool. Additionally, because BIOME-BGC assumes that canopy water must be evaporated before stomatal conductance occurs (diffusion through water is 10,000 times slower than through air), canopy water interception directly impacts transpiration. For BIOME-BGC parameterization, field studies must include measurements of leaf area index and daily canopy interception. Such work is rare and results are highly dependent on the methodology used (Crockford and Richardson 1990). Nonetheless, reported values fell within a relatively narrow range. We were unable to locate any studies providing the required information for grass canopies and based on a generally erectophile leaf orientation, we set grass  $W_{\text{int}}$  to 50% of the forest value.

ENF, DNF, DBF, and shrub	Mean = 0.045, std dev = 0.012, $n = 5$	
<i>Pinus radiata</i>	0.036	(Kelliher et al. 1992)
<i>Pinus</i>	0.052	(Gash et al. 1995)
Temperate broadleaf	0.035	(Klaassen et al. 1996)
Temperate broadleaf	0.040	(Lankreijer et al. 1993)
Tropical broadleaf	0.063	(Scatena 1990)
Grass	Set to 50% of above mean	

### A.7.2 Light extinction coefficient

The canopy light extinction coefficient ( $k$ , defined as the mean projection of the unit foliage area on the plane normal to incident radiation, unitless) controls canopy photosynthetically active radiation absorption. Measurements of  $k$  are abundant and most are based on the adoption of Beer's law in Monsi et al. (Monsi et al. 1953):  $k = \{-\ln(I_i/I_o)\} / \text{LAI}$ , where  $k$  is the extinction coefficient,  $I_i$  is the below-canopy radiation,  $I_o$  is the above-canopy radiation, and LAI is leaf area index. Measurements of  $I_i/I_o$  are usually made with a radiation-measuring device such as a sunfleck ceptometer (Decagon Instruments, Pullman, WA). LAI has been measured with many techniques, including litterfall (Heilman and Fu-Guang 1994), radiation transmittance (Chen et al. 1997), sapwood allometrics (Pierce et al. 1994; Sampson and Smith 1993), and foliage biomass (Sampson and Allen 1998). Alternatively,  $k$  can be calculated through physical measurement of the contact frequency (Norman and Campbell 1989) as in Groeneveld (Groeneveld 1997). The value of  $k$  is known to vary with solar angle in planophile (needle leaf) canopies (Black et al. 1991) but not in canopies with random (broad leaf) foliage orientation (Chen et al. 1997). Additionally,  $k$  appears to decrease with stand age as a result of changes in three-dimensional canopy structure (Brown and Parker 1994; Heilman and Fu-Guang 1994). Literature values of  $k$  were therefore drawn from a strikingly diverse pool of methodologies and stand conditions. As leaf morphology, not phenology, is the primary determinant of  $k$ , we included evergreen broad leaf values in the DBF calculation. We report values based on

measurements taken around solar noon or corrected to nadir values with the cosine of the solar elevation angle correction:  $k = \{-\ln(I_i/I_o) \cos \theta\}/\text{LAI}$ , where  $\theta$  is the solar elevation angle (0 directly overhead). The data showing all biomes at or near 0.5 support the statement in Chen et al. (Chen 1997) that 0.5 can be taken as a first approximation of  $k$  for almost all types of canopies.

ENF	Mean = 0.51, std dev = .052, $n = 14$	
ENF	0.530	(Pierce and Running 1988)
ENF	0.490	(Pierce and Running 1988)
ENF	0.510	(Pierce and Running 1988)
ENF	0.480	(Pierce and Running 1988)
ENF	0.480	(Pierce and Running 1988)
ENF	0.520	(Pierce and Running 1988)
ENF	0.580	(Pierce and Running 1988)
<i>Pinus</i>	0.460	(Sinclair and Knoer 1982)
<i>Pinus</i>	0.529	(Lindroth and Perttu 1981)
<i>Pinus contorta</i>	0.430	(Sampson and Smith 1993)
<i>Pinus taeda</i>	0.511	(Sampson and Allen 1998)
<i>Pinus taeda</i>	0.477	(Sampson and Allen 1998)
<i>Pinus taeda</i>	0.641	(Sampson and Allen 1998)
<i>Pseudotsuga menziesii</i>	0.500	(Black et al. 1991)
DNF	0.51	Set to ENF
DBF	Mean = 0.54, std dev = 0.079, $n = 11$	
<i>Castanopsis</i>	0.500	(Waring and Schlesinger 1985)
<i>Eucalyptus globulus</i>	0.500	(Gazarini et al. 1990)
<i>Fagus</i>	0.400	(Waring and Schlesinger 1985)
Mixed deciduous	0.660	(Brown and Parker 1994)
<i>Populus deltoides</i>	0.540	(Li et al. 1997)
<i>Populus hybrid</i>	0.622	(Heilman and Fu-Guang 1994)
<i>Populus hybrid</i>	0.473	(Heilman and Fu-Guang 1994)
<i>Populus tremuloides</i>	0.500	(Chen et al. 1997)
Rain forest	0.600	(Waring and Schlesinger 1985)
<i>Theobroma cacao</i>	0.610	(Miyaji et al. 1997)
Tropical deciduous forest	0.610	(Maass et al. 1995)
Grass	Mean = 0.48, std dev = 0.13, $n = 21$	
<i>Cynodon dactylon</i>	0.620	(Morgan and Brown 1983)
<i>Distichlis spicata</i>	0.557	(Groeneveld 1997)
<i>Festuca arundinacea</i>	0.439	(Sugiyama et al. 1985)
<i>Festuca arundinacea</i>	0.411	(Sugiyama et al. 1985)
<i>Festuca arundinacea</i>	0.401	(Sugiyama et al. 1985)
<i>Festuca arundinacea</i>	0.406	(Sugiyama et al. 1985)
<i>Festuca arundinacea</i>	0.322	(Sugiyama et al. 1985)
<i>Festuca arundinacea</i>	0.533	(Sugiyama et al. 1985)
<i>Festuca arundinacea</i>	0.550	(Sugiyama et al. 1985)
<i>Festuca arundinacea</i>	0.372	(Sugiyama et al. 1985)
<i>Festuca arundinacea</i>	0.514	(Sugiyama et al. 1985)
<i>Festuca arundinacea</i>	0.441	(Sugiyama et al. 1985)
<i>Festuca arundinacea</i>	0.533	(Sugiyama et al. 1985)
<i>Festuca arundinacea</i>	0.369	(Sugiyama et al. 1985)
<i>Festuca arundinacea</i>	0.384	(Sugiyama et al. 1985)
<i>Festuca arundinacea</i>	0.594	(Sugiyama et al. 1985)
<i>Festuca arundinacea</i>	0.314	(Sugiyama et al. 1985)

Grass	Mean = 0.48, std dev = 0.13, $n = 21$		(Continued)
<i>Pennisetum</i>	0.400	(Matsuda et al. 1991)	
<i>Sasa nipponica</i>	0.742	(Agata and Kamata 1979)	
<i>Sasa nipponica</i>	0.778	(Agata and Kamata 1979)	
<i>Sporobolus airoides</i>	0.490	(Groeneveld 1997)	
Shrub	Mean = 0.55, std dev = 0.10, $n = 8$		
<i>Artemesia tridentata</i>	0.411	(Groeneveld 1997)	
<i>Atriplex canescens</i>	0.531	(Groeneveld 1997)	
<i>Atriplex confertifolia</i>	0.531	(Groeneveld 1997)	
<i>Atriplex lentiformis</i>	0.528	(Groeneveld 1997)	
<i>Chrysothamnus nauseosus</i>	0.531	(Groeneveld 1997)	
<i>Lysimachia vulgaris</i>	0.689	(Hirose et al. 1988)	
<i>Lysimachia vulgaris</i>	0.716	(Hirose et al. 1988)	
<i>Sarcobatus vermiculatus</i>	0.470	(Groeneveld 1997)	

### A.7.3 Percent of leaf nitrogen in Rubisco

Rubisco, the enzyme catalyzing the binding of  $\text{CO}_2$ , is probably the most abundant protein on Earth. The percent of leaf nitrogen in Rubisco (PLNR, percent) controls potential rates of carboxylation and is, therefore, a dominant control of canopy assimilation. While some data for PLNR do exist, especially for crops, there are insufficient field data with which to parameterize natural vegetation types. PLNR can be related to more commonly measured parameters through the following equation:  $\text{PLNR} = (V_{c_{\max}} \text{ SLA } C:N_{\text{leaf}}) / (\Gamma \text{ act})$ , where  $V_{c_{\max}}$  is the maximum rate of carboxylation ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), SLA is the specific leaf area ( $\text{m}^2 \text{ kg C}^{-1}$ ),  $C:N_{\text{leaf}}$  is the leaf C:N ratio ( $\text{kg C kg N}^{-1}$ ),  $\Gamma$  is the ratio of the mass of Rubisco to the mass of nitrogen in Rubisco [ $7.16 \text{ kg Rubisco kg N in Rubisco}^{-1}$  (Kuehn and McFadden 1969)], and act is the Rubisco activity at  $25^\circ\text{C}$  [ $60,000 \mu\text{mol CO}_2 \text{ kg Rubisco}^{-1} \text{ s}^{-1}$  (Woodrow and Berry 1988)]. PLNR is in units of kilograms of nitrogen in Rubisco per kilograms of leaf nitrogen, or a dimensionless fraction. Wullschleger (Wullschleger 1993) summarized  $V_{c_{\max}}$  data for a wide variety of species. We calculated ENF and DBF PLNR from  $V_{c_{\max}}$  summaries in Wullschleger (Wullschleger 1993) and SLA and  $C:N_{\text{leaf}}$  presented above. Wullschleger reported that measurement temperatures for ENF were generally lower than for other biomes, possible underpredicting  $V_{c_{\max}}$ . We therefore adjusted ENF  $V_{c_{\max}}$  to the mean plus one  $\sigma$ . We calculated a mean value for grass  $V_{c_{\max}}$  from data presented in (Wullschleger 1993). Shrub  $V_{c_{\max}}$  data were limited to hot shrubs and we chose to set shrub PLNR to the ENF value. Due to its high maximum rates of photosynthesis (Gower and Richards 1990), we set DNF PLNR to the DBF value.

Calculated PLNR data appeared to be within the range reported in the literature. In annual grasses, PLNR was 0.15 for *Abutilon theophrasti* and 0.09 for *Amaranthus retroflexus* (Tissue et al. 1995). PLNR was 0.17 in a fertilized *Populus* hybrid [(Brendley and Pell 1998); fertilization raises Rubisco investment], 0.11 in *Alocasia macrorrhiza*, an Australian tropical understory species (Seeman 1989), and 0.0457 in 1-yr-old needles of *Pinus radiata* (Thurnbull et al. 1998). Crop values generally range from 0.15 to 0.30 (Makino et al. 1994; Makino et al. 1992).

## Appendix B: Notation

Symbol	Definition	Units
$A_{\text{gmax}}$	Maximum net canopy assimilation rate	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
C	Carbon	Unitless
$\text{C:N}_{\text{dw}}$	Dead wood carbon to nitrogen ratio	$\text{kg C (kg N)}^{-1}$
$\text{C:N}_{\text{fr}}$	Fine root carbon to nitrogen ratio	$\text{kg C (kg N)}^{-1}$
$\text{C:N}_{\text{leaf}}$	Leaf carbon to nitrogen ratio	$\text{kg C (kg N)}^{-1}$
$\text{C:N}_{\text{lit}}$	Litter carbon to nitrogen ratio	$\text{kg C (kg N)}^{-1}$
$\text{C:N}_{\text{lw}}$	Live wood carbon to nitrogen ratio	$\text{kg C (kg N)}^{-1}$
CRC:SC	New coarse root carbon to new stem carbon allocation ratio	$\text{kg C (kg C)}^{-1}$
C3G	C <sub>3</sub> grassland	Unitless
C4G	C <sub>4</sub> grassland	Unitless
DBF	Deciduous broad leaf forest	Unitless
DNF	Deciduous needle leaf forest	Unitless
$\text{DW}_{\text{cel}}$	Dead wood cellulose	%
$\text{DW}_{\text{lig}}$	Dead wood lignin	%
ENF	Evergreen needle leaf forest	Unitless
FM	Fire mortality	$1 \text{ yr}^{-1}$
FRC:LC	New fine root carbon to new leaf carbon allocation ratio	$\text{kg C (kg C)}^{-1}$
$\text{FR}_{\text{cel}}$	Fine root cellulose	%
$\text{FR}_{\text{lab}}$	Fine root labile	%
$\text{FR}_{\text{lig}}$	Fine root lignin	%
$g$	Conductance	$\text{m s}^{-1}$
$g_{\text{bl}}$	Boundary layer conductance	$\text{m s}^{-1}$
$g_{\text{cut}}$	Cuticular conductance	$\text{m s}^{-1}$
$g_{\text{smax}}$	Maximum stomatal conductance	$\text{m s}^{-1}$
$k$	Light extinction coefficient	Unitless
LAI	Leaf area index	$\text{m}^2 \text{ m}^{-2}$
$\text{LAI}_{\text{all:proj}}$	All-sided to projected LAI ratio	$\text{LAI LAI}^{-1}$
$\text{L}_{\text{cel}}$	Litter cellulose	%
LFRT	Leaf and fine root turnover	$1 \text{ yr}^{-1}$
$\text{L}_{\text{lab}}$	Litter labile	%
$\text{L}_{\text{lig}}$	Litter lignin	%
LWC:TWC	New live wood carbon to new total wood carbon allocation ratio	$\text{kg C (kg C)}^{-1}$
LWT	Live wood turnover	$1 \text{ yr}^{-1}$
N	Nitrogen	Unitless
PLNR	Percent of leaf nitrogen in Rubisco	%
Rubisco	Ribulose-1,5-bisphosphate carboxylase/oxygenase	Unitless
SC:LC	New stem carbon to new leaf carbon allocation ratio	$\text{kg C (kg C)}^{-1}$
SLA	Specific leaf area	$\text{m}^{-2} \text{ kg C}$
$\text{SLA}_{\text{shd:sun}}$	Shaded to sunlit SLA ratio	$\text{SLA SLA}^{-1}$
SOILC	Soil carbon	$\text{kg C m}^{-2}$
$V_{\text{cmax}}$	Maximum rate of carboxylation	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
VEMAP	Vegetation/Ecosystem Modeling and Analysis Project	Unitless
VPD	Vapor pressure deficit	kPa
$\text{VPD}_{\text{f}}$	VPD at final reduction of stomatal conductance	kPa



Symbol	Definition	Units	(Continued)
$VPD_i$	VPD at initial reduction of stomatal conductance	kPa	
$W_{int}$	Water interception coefficient	$1 \text{ LAI}^{-1} \text{ day}^{-1}$	
WOODC	Wood carbon	$\text{kg C m}^{-2}$	
WPM	Whole plant mortality	$1 \text{ yr}^{-1}$	
$\Psi$	Water potential	MPa	
$\Psi_f$	Predawn leaf water potential at final reduction of stomatal conductance	MPa	
$\Psi_i$	Predawn leaf water potential at initial reduction of stomatal conductance	MPa	
$\Psi_l$	Leaf water potential	MPa	
$\Psi_{lpd}$	Predawn leaf water potential	MPa	
$\Psi_s$	Soil water potential	MPa	
$\delta_{bl}$	Leaf boundary layer	mm	

Appendix C: Site Locations and Climate

Site distribution generally encompassed the climatic range of each biome (Table C1). ENF geographic distribution was widest, ranging from western to eastern forests in inland and coastal areas. DNF was concentrated in a broad longitudinal band at the northern limit of the United States. DBF was distributed throughout the eastern United States, with a coastal western site. C3G and C4G together had broad coverage of the entire north–south-central U.S. grasslands. Shrubs were concentrated in the western United States and ranged from cold to warm climates.

Table C1. Locations and climate of simulation pixels for sensitivity analysis: Tann, mean annual temperature (°C); Prcp, mean annual precipitation (cm); VP, mean annual water vapor pressure (Pa); SW, annual average day-light shortwave radiation ( $\text{W m}^{-2}$ ).

	Latitude	Longitude	Tann	Prcp	VP	SW
ENF						
1	48.75	−120.25	4.1	86.5	504.8	340.9
2	48.25	−121.75	8.3	230.0	802.3	296.6
3	47.75	−93.25	3.1	65.7	607.0	317.4
4	47.25	−123.75	9.5	304.0	889.5	287.0
5	44.75	−118.75	5.8	59.1	517.6	371.7
6	44.75	−73.25	7.1	80.7	835.3	307.2
7	37.25	−77.25	14.8	108.4	1239.7	368.2
8	34.25	−107.25	11.5	28.5	516.7	509.1
9	32.75	−87.75	17.5	131.8	1449.1	392.0
10	31.75	−110.75	15.9	47.8	851.5	480.4
Mean			9.7	114.2	821.4	367.1
DNF						
1	48.75	−113.75	1.9	153.3	504.8	332.4
2	47.25	−115.75	5.9	116.1	660.2	304.7
3	46.25	−84.75	4.8	79.9	679.3	309.8
74	45.75	−67.75	5.1	102.6	683.5	328.8
5	45.25	−118.75	6.7	63.5	591.6	348.1

Table C1. (Continued)

I	Latitude	Longitude	Tann	Prcp	VP	SW
6	45.25	−106.75	6.7	39.1	546.7	382.8
7	44.75	−119.25	7.6	38.7	513.3	385.6
8	44.75	−89.25	6.0	79.9	753.5	328.2
9	44.75	−72.75	5.1	111.0	731.0	324.3
10	44.25	−109.75	0.5	73.7	408.8	382.3
Mean			5.0	85.8	607.3	342.7
DBF						
1	43.25	−82.75	8.1	73.0	822.5	335.8
2	43.25	−70.75	8.1	110.2	820.7	335.8
3	39.25	−121.25	15.3	95.6	863.2	392.3
4	39.25	−78.25	11.4	96.4	985.1	363.9
5	37.75	−93.25	13.2	104.8	1133.8	373.8
6	33.75	−80.25	17.5	114.6	1411.2	396.0
7	32.25	−84.25	18.1	118.6	1476.7	393.7
8	31.75	−87.25	18.1	138.7	1490.0	403.2
9	30.25	−96.25	19.9	100.7	1606.5	393.6
10	28.25	−82.25	22.1	135.4	1863.7	398.1
Mean			15.2	108.8	1247.3	378.6
C3G						
1	45.25	−104.25	6.4	35.8	568.3	372.2
2	43.25	−97.75	8.7	58.0	819.8	356.3
3	41.75	−106.25	5.3	29.6	433.2	419.5
4	40.25	−107.75	4.6	48.5	440.4	446.4
5	40.25	−99.75	11.1	55.1	861.1	391.9
6	39.75	−88.75	11.7	96.4	1069.6	352.7
7	38.25	−96.25	12.9	89.8	1114.8	370.1
8	36.75	−97.75	15.0	75.9	1195.7	384.4
9	33.75	−103.75	14.3	38.3	762.2	469.8
10	33.75	−100.75	16.5	54.0	1071.2	431.9
Mean			10.6	58.0	833.6	399.5
C4G						
1	42.75	−98.25	9.2	58.0	849.9	351.2
2	38.75	−99.25	12.2	57.7	936.2	393.9
3	36.25	−102.75	12.9	37.6	741.6	454.8
4	36.25	−100.75	13.8	49.6	920.4	429.7
5	35.75	−98.25	15.6	70.8	1215.8	387.9
6	33.75	−101.25	15.2	50.0	953.7	441.2
7	33.25	−102.75	14.8	43.1	816.0	473.9
8	31.75	−102.25	17.7	34.7	934.2	459.6
9	29.75	−94.25	20.3	132.5	1816.1	364.2
10	29.25	−100.25	20.2	52.9	1328.3	429.6
Mean			15.2	58.8	1051.2	418.6
Shrub						
1	44.75	−121.25	9.6	32.9	514.4	374.0
2	44.25	−112.25	4.8	36.1	477.6	384.8
3	42.25	−119.75	7.6	28.1	442.7	408.8
4	40.25	−118.25	9.6	22.3	429.1	450.6
5	40.25	−109.25	8.0	22.6	428.3	448.0
6	39.75	−112.75	9.9	23.4	513.5	428.1
7	39.25	−119.25	10.1	19.3	422.2	451.8

Table C1. (Continued)

	Latitude	Longitude	Tann	Prcp	VP	SW
8	39.25	−112.25	9.1	35.8	555.9	432.5
9	34.75	−119.75	12.6	54.8	553.6	482.2
10	29.75	−103.75	17.7	32.9	826.5	508.8
Mean			9.9	30.7	516.4	437.0

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**Table 1. Mean BIOME-BGC parameter values for evergreen needle leaf forest (ENF), shrub, deciduous needle leaf forest (DNF), deciduous broadleaf forest (DBF), and grass biomes. Parameter descriptions and individual values are presented in appendix A.**

Parameter (C = carbon, N = nitrogen)	ENF	Shrub	DNF	DBF	Grass
Leaf and fine root turnover (LFRT) <sup>a</sup>	0.26	0.26	1.0	1.0	1.0
Live wood turnover (LWT) <sup>a</sup>	0.70	0.70	0.70	0.70	
Fire mortality (FM) <sup>a</sup>	5.0E–3	0.010	5.0E–3	2.5E–3	5.0E–2
Whole plant mortality (WPM) <sup>a</sup>	5.0E–3	0.020	5.0E–3	5.0E–3	0.10
New fine root C to new leaf C ratio (FRC:LC) <sup>b</sup>	1.4	1.4	1.4	1.2	1.0
New stem C to new leaf C ratio (SC:LC) <sup>b</sup>	2.2	0.22	2.2	2.2	
New live wood C to new total wood C ratio (LWC:TWC) <sup>b</sup>	0.071	1.0	0.071	0.16	
New coarse root C to new stem C ratio (CRC:SC) <sup>b</sup>	0.29	0.29	0.29	0.22	
Leaf C:N (C:N <sub>leaf</sub> ) <sup>c</sup>	42	35	27	25	25
Litter C:N (C:N <sub>lit</sub> ) <sup>c</sup>	93	75	120	55	45
Fine root C:N (C:N <sub>fr</sub> ) <sup>c</sup>	58	58	58	48	50
Live wood C:N (C:N <sub>lw</sub> ) <sup>c</sup>	50	50	50	50	
Dead wood C:N (C:N <sub>dw</sub> ) <sup>c</sup>	730	730	730	550	
Fine root labile (FR <sub>lab</sub> ) <sup>d</sup>	34	34	34	34	34
Fine root cellulose (FR <sub>cel</sub> ) <sup>d</sup>	44	44	44	44	44
Fine root lignin (FR <sub>lig</sub> ) <sup>d</sup>	22	22	22	22	22
Litter labile (L <sub>lab</sub> ) <sup>d</sup>	31	56	31	38	68
Litter cellulose (L <sub>cel</sub> ) <sup>d</sup>	45	29	45	44	23
Litter lignin (L <sub>lig</sub> ) <sup>d</sup>	24	15	24	18	9.0
Dead wood cellulose (DW <sub>cel</sub> ) <sup>d</sup>	71	71	71	77	
Dead wood lignin (DW <sub>lig</sub> ) <sup>d</sup>	29	29	29	23	
Specific leaf area (SLA) <sup>e</sup>	8.2	12	22	32	49
All-sided to projected leaf area ratio (LAI <sub>all:proj</sub> ) <sup>f</sup>	2.6	2.3	2.6	2.0	2.0
Shaded to sunlit specific leaf area ratio (SLA <sub>shd:sun</sub> ) <sup>g</sup>	2.0	2.0	2.0	2.0	2.0
Maximum stomatal conductance (g <sub>smax</sub> ) <sup>h</sup>	6.0E–3	6.0E–3	6.0E–3	6.0E–3	6.0E–3
Cuticular conductance (g <sub>cut</sub> ) <sup>h</sup>	6.0E–5	6.0E–5	6.0E–5	6.0E–5	6.0E–5
Boundary layer conductance (g <sub>bl</sub> ) <sup>h</sup>	0.09	0.02	0.09	0.01	0.04
Leaf water potential at initial g <sub>smax</sub> reduction (LWP <sub>i</sub> ) <sup>i</sup>	-0.65	-0.81	-0.65	-0.34	-0.73
Leaf water potential at final g <sub>smax</sub> reduction (LWP <sub>f</sub> ) <sup>i</sup>	-2.5	-4.2	-2.5	-2.2	-2.7
Vapor pressure deficit at initial g <sub>smax</sub> reduction (VPD <sub>i</sub> ) <sup>j</sup>	0.61	0.97	0.61	1.1	1.0
Vapor pressure deficit at final g <sub>smax</sub> reduction (VPD <sub>f</sub> ) <sup>j</sup>	3.1	4.1	3.1	3.6	5.0
Water interception coefficient (W <sub>int</sub> ) <sup>k</sup>	0.045	0.045	0.045	0.045	0.022
Light extinction coefficient (k) <sup>l</sup>	0.51	0.55	0.51	0.54	0.48
Percent of leaf N in Rubisco (PLNR) <sup>d</sup>	3.3	3.3	8.8	8.8	21

Unit key: <sup>a</sup> = 1 yr<sup>-1</sup>, <sup>b</sup> = kg C kg C<sup>-1</sup>, <sup>c</sup> = kg C kg N<sup>-1</sup>, <sup>d</sup> = percent, <sup>e</sup> = m<sup>2</sup> kg C<sup>-1</sup>, <sup>f</sup> = LAI LAI<sup>-1</sup>, <sup>g</sup> = SLA SLA<sup>-1</sup>, <sup>h</sup> = m s<sup>-1</sup>, <sup>i</sup> = MPa, <sup>j</sup> = kPa, <sup>k</sup> = 1 LAI<sup>-1</sup> day<sup>-1</sup>, <sup>l</sup> = unitless.



Table 2. Effect of varying input parameters in evergreen needle leaf (ENF), shrub, deciduous needle leaf (DNF), deciduous broad leaf (DBF), C<sub>3</sub> grass (C3G), and C<sub>4</sub> grass (C4G) biomes. Here, Δ = change in simulated mean annual 1895–1993 net primary production (NPP, g m<sup>-2</sup>) caused by increasing the parameter from the mean minus 20% to the mean plus 20%. Each value represents the mean from 10 pixels per biome. Only those parameters significantly affecting at least one biome are shown. LFRT not varied for deciduous biomes.

	ENF	Shrub	DNF	DBF	C3G	C4G
C:N <sub>leaf</sub>	-87 <sup>a</sup>	-24 <sup>a</sup>	-80 <sup>a</sup>	-63 <sup>a</sup>	31 <sup>a</sup>	36 <sup>a</sup>
C:N <sub>fr</sub>	72 <sup>a</sup>	19 <sup>a</sup>	24 <sup>c</sup>	42 <sup>a</sup>	26 <sup>a</sup>	30 <sup>a</sup>
LFRT	43 <sup>a</sup>	4 <sup>c</sup>				
FRC:LC	-56 <sup>a</sup>	-16 <sup>a</sup>	-48 <sup>a</sup>	-18 <sup>c</sup>	6 <sup>c</sup>	8 <sup>b</sup>
SLA	-64 <sup>a</sup>	-11 <sup>a</sup>	-29 <sup>b</sup>	-62 <sup>a</sup>	-5 <sup>c</sup>	-2 <sup>c</sup>
g <sub>smax</sub>	-61 <sup>a</sup>	-14 <sup>a</sup>	-45 <sup>a</sup>	-38 <sup>a</sup>	-7 <sup>b</sup>	1 <sup>c</sup>
LAI <sub>all:proj</sub>	-41 <sup>a</sup>	-2 <sup>c</sup>	0 <sup>c</sup>	0 <sup>c</sup>	0 <sup>c</sup>	0 <sup>c</sup>
PLNR	142 <sup>a</sup>	37 <sup>a</sup>	104 <sup>a</sup>	104 <sup>a</sup>	4 <sup>c</sup>	-1 <sup>c</sup>
FR <sub>cel</sub>	0 <sup>c</sup>	0 <sup>c</sup>	21 <sup>c</sup>	5 <sup>c</sup>	27 <sup>a</sup>	32 <sup>a</sup>
FR <sub>lig</sub>	0 <sup>c</sup>	0 <sup>c</sup>	-19 <sup>c</sup>	-5 <sup>c</sup>	-21 <sup>a</sup>	-27 <sup>a</sup>
W <sub>int</sub>	-41 <sup>a</sup>	-2 <sup>c</sup>	-16 <sup>c</sup>	-31 <sup>b</sup>	-1 <sup>c</sup>	0 <sup>c</sup>
K	7 <sup>c</sup>	-3 <sup>c</sup>	17 <sup>c</sup>	-54 <sup>a</sup>	0 <sup>c</sup>	-2 <sup>c</sup>
FR <sub>lab</sub>	0 <sup>c</sup>	0 <sup>c</sup>	15 <sup>c</sup>	2 <sup>c</sup>	13 <sup>a</sup>	14 <sup>a</sup>
L <sub>cel</sub>	0 <sup>c</sup>	0 <sup>c</sup>	9 <sup>c</sup>	4 <sup>c</sup>	10 <sup>a</sup>	13 <sup>a</sup>
FM	-1 <sup>c</sup>	0 <sup>c</sup>	-23 <sup>c</sup>	-3 <sup>c</sup>	-58 <sup>a</sup>	-73 <sup>a</sup>
L <sub>lab</sub>	0 <sup>c</sup>	0 <sup>c</sup>	4 <sup>c</sup>	1 <sup>c</sup>	16 <sup>a</sup>	17 <sup>a</sup>

<sup>a</sup> Significant at the 1% level.

<sup>b</sup> Significant at the 5% level.

<sup>c</sup> Not significant.

Table 3. Design of the 2<sup>5-1</sup> half-fraction factorial sensitivity analysis for ENF and C3G biomes. Columns two–six show contrast coefficients for the five parameters in the analysis (different for ENF and C3G). A plus symbol indicates that the parameter was set at the mean plus the standard error while a minus symbol indicates mean minus standard error. When C3G FR<sub>cel</sub> and L<sub>cel</sub> were set to +, FR<sub>lig</sub> and L<sub>lig</sub> were reduced by equal magnitude; thus +FR<sub>cel</sub> and +L<sub>cel</sub> indicate high quality litter and -FR<sub>cel</sub> and -L<sub>cel</sub> indicate the reverse. The ENF and C3G columns under the mean NPP section show the mean NPP (g m<sup>-2</sup>) from the simulation using the parameter levels of columns two–six. For example, simulation 1 had C:N<sub>leaf</sub>, g<sub>smax</sub>, PLNR, and SLA at low levels and C:N<sub>fr</sub> at a high level and produced a mean 99-yr NPP for the 10 ENF pixels of 441 g m<sup>-2</sup>.

Parameter contrast coefficient						Mean NPP	
ENF	C:N <sub>leaf</sub>	g <sub>smax</sub>	PLNR	SLA	C:N <sub>fr</sub>	ENF	C3G
C3G	C:N <sub>leaf</sub>	FM	FR <sub>cel</sub>	L <sub>cel</sub>	C:N <sub>fr</sub>		
1	-	-	-	-	+	441	228
2	+	-	-	-	-	375	220
3	-	+	-	-	-	388	193
4	+	+	-	-	+	400	212
5	-	-	+	-	-	472	229

Table 3. (Continued)

ENF C3G	Parameter contrast coefficient					Mean NPP	
	C:N <sub>leaf</sub> C:N <sub>leaf</sub>	$g_{smax}$ FM	PLNR FR <sub>cel</sub>	SLA L <sub>cel</sub>	C:N <sub>fr</sub> C:N <sub>fr</sub>	ENF	C3G
6	+	-	+	-	+	493	247
7	-	+	+	-	+	498	218
8	+	+	+	-	-	439	216
9	-	-	-	+	-	381	225
10	+	-	-	+	+	392	245
11	-	+	-	+	+	403	217
12	+	+	-	+	-	342	209
13	-	-	+	+	+	487	253
14	+	-	+	+	-	430	245
15	-	+	+	+	-	437	221
16	+	+	+	+	+	453	241

Table 4. Main effects of parameter variation in ENF and C3G biomes. Effect columns show the expected effect on NPP ( $\text{g m}^{-2}$ ) of raising a parameter from the mean minus standard error to the mean plus standard error. Values are mean and 95% confidence interval calculated from the  $t$  distribution with nine degrees of freedom.

ENF		C3G	
Parameter	Effect	Parameter	Effect
C:N <sub>leaf</sub>	$-23.1 \pm 7.9$	C:N <sub>leaf</sub>	$6.6 \pm 1.8$
$g_{smax}$	$-13.9 \pm 3.6$	FM	$-20.6 \pm 3.4$
PLNR	$73.3 \pm 23.1$	FR <sub>cel</sub>	$15.0 \pm 3.8$
SLA	$-22.6 \pm 7.0$	L <sub>cel</sub>	$11.6 \pm 2.9$
C:N <sub>fr</sub>	$37.9 \pm 14.5$	C:N <sub>fr</sub>	$13.0 \pm 3.8$

Table 5. Two-way interaction effects of parameter variation in ENF and C3G biomes. The interaction columns show the expected interaction effect on NPP ( $\text{g m}^{-2}$ ) caused by raising the shown parameters from mean minus standard error to mean plus standard error. Values are mean and 95% confidence interval calculated from the  $t$  distribution with nine degrees of freedom (\* indicates significant interaction effect).

ENF		C3	
Parameters	Interaction	Parameters	Interaction
C:N <sub>leaf</sub> $\times$ $g_{smax}$	$-0.2 \pm 0.9$	C:N <sub>leaf</sub> $\times$ 9.1.1.4	$0.7 \pm 1.4$
C:N <sub>leaf</sub> $\times$ PLNR*	$2.9 \pm 2.5$	C:N <sub>leaf</sub> $\times$ FR <sub>cel</sub>	$0.5 \pm 0.9$
C:N <sub>leaf</sub> $\times$ 9.1.1.1.2	$-0.1 \pm 0.5$	C:N <sub>leaf</sub> $\times$ L <sub>cel</sub>	$-0.6 \pm 1.1$
C:N <sub>leaf</sub> $\times$ C:N <sub>fr</sub>	$0.1 \pm 0.7$	C:N <sub>leaf</sub> $\times$ C:N <sub>fr</sub>	$0.8 \pm 1.1$
$g_{smax}$ $\times$ PLNR	$0.2 \pm 1.1$	FM $\times$ FR <sub>cel</sub>	$1.3 \pm 2.9$
$g_{smax}$ $\times$ SLA	$0.1 \pm 0.5$	FM $\times$ L <sub>cel</sub>	$0.4 \pm 1.4$
$g_{smax}$ $\times$ C:N <sub>fr</sub> *	$-0.7 \pm 0.2$	FM $\times$ C:N <sub>fr</sub>	$-0.5 \pm 1.1$
PLNR $\times$ 1.1.1.1.3	$-1.0 \pm 1.1$	FR <sub>cel</sub> $\times$ L <sub>cel</sub>	$0.9 \pm 1.1$

Table 6. Comparison of parameterization schemes. Spatial prediction refers to a mean value calculated from Figure 3 or Figure 4; single value per biome refers to the mean value calculated from the literature searches described in the preceding sections. Parameters are leaf carbon to nitrogen ratio ( $C:N_{leaf}$ , kg C kg N<sup>-1</sup>), specific leaf area (SLA, m<sup>2</sup> kg C<sup>-1</sup>), leaf life span (months), and the percent of leaf nitrogen in Rubisco (PLNR, dimensionless). Biomes are evergreen needle leaf forest (ENF) and deciduous broad leaf forest (DBF). DBF leaf life span from BIOME-BGC phenology model (White et al. 1997).

	ENF		DBF	
	Spatial prediction	Single value per biome	Spatial prediction	Single value per biome
$C:N_{leaf}$	50	42	33	25
SLA	9.2	8.2	16	32
Leaf life span	47	46	13	6.6
PLNR	3.9	3.3	5.5	8.8

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