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Ecophysiological Parameters for Pacific Northwest Trees

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Abstract

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We developed a species- and location-specific database of published ecophysiological variables typically used as input parameters for biogeochemical models of coniferous and deciduous forested ecosystems in the Western United States. Parameters are based on the requirements of Biome-BGC, a widely used biogeochemical model that was originally parameterized for the forests of the Pacific Northwest. Several other ecosystem models, including Century 5, Daycent, TEM, and PnET, also use some of the inputs described here. This database provides a compendium of ecophysiological data for the Pacific Northwest that will provide easily accessible information for particular tree species, parameters, and ecosystems for application to simulation modeling.

Keywords: Ecological modeling, ecophysiology, Pacific Northwest forests.

Summary

Ecosystem models use input parameters including physiology, biochemistry, structure, and allocation to describe processes and fluxes such as productivity, nitrogen cycling, and water relations. Many ecosystem models useful for investigating these interactions are grounded in ecophysiological relationships originally measured in the laboratory or field, typically at scales ranging from the leaf to the plot level. These lab- or field-based measurements serve as both parameterization and validation data sets for ecosystem models and therefore play a crucial role in current and future model development and implementation.

Ecophysiological parameters for biogeochemical models have been measured for Pacific Northwest tree species on a variety of sites with multiple age classes. However, locating these parameter values in the literature can be difficult and time consuming especially when multiple species or community types are included in a model. Furthermore, these values may have been measured by using different methods or recorded in different units.

We developed a summary of critical ecophysiological values for biogeochemical model parameters through a search of the scientific literature and expert opinion. Parameters are based on the requirements of Biome-BGC, a widely used biogeochemical model that was originally parameterized for the forests of the Pacific Northwest. Having this information in an easily accessible database will make future modeling efforts with Biome-BGC and other models more efficient and consistent.

Introduction

Recent efforts to model rapid changes in global climate and atmospheric biochemistry require a detailed understanding of how biochemistry, biophysics, and plant responses interact across local, regional, and global scales (Waring 1993). Although some of these interactions can be measured at local scales, empirical estimates of these processes at regional and global scales are not yet tenable. Simulation modeling provides an essential tool for exploring these complex interactions at larger spatial scales (Running 1994). Ecosystem models use input parameters including physiology, biochemistry, structure, and allocation to describe processes and fluxes such as productivity, nitrogen cycling, and water relations. Many ecosystem models useful for investigating these interactions are grounded in ecophysiological relationships originally measured in the laboratory or field, typically at scales ranging from the leaf to the plot level. These lab- or field-based measurements serve as both parameterization and validation data sets for ecosystem models and therefore play a crucial role in current and future model development and implementation.

Ecophysiological relationships of forest ecosystems, especially in the Pacific Northwest of North America, have been studied extensively. Many critical ecophysiological parameters for biogeochemical models have been measured for individual species on a variety of sites with various age classes present. However, locating these parameter values in the literature can be difficult and time consuming, especially when multiple species or community types are included in a model run (Running 1994). Although data exist for many species, these values are difficult to locate and standardize for several reasons: (1) data were printed in older publications (pre-1980) that are not catalogued in online databases; (2) data were published in obscure journals or gray literature; (3) data collection methods and units differ substantially for some parameters, making standardization difficult. Despite these difficulties, it is critical that important parameter values and all references for these parameter values be provided for any model-based study (Aber 1997, White et al. 2000).

In biome-based ecosystem models, commonly measured ecophysiological variables taken from a large number of observations of many communities and locations are typically averaged across broad vegetation classes (e.g., evergreen needleleaf, broadleaf deciduous, etc.) to generate default parameterization values (Neilson 1995, White et al. 2000). These default values may include data collected from low-elevation to subalpine locations, mesic to xeric sites, and recently disturbed to old-growth forests. Thus, the average or default values include a high degree of variability even within these broad vegetation types. New parameterization data sets may be required to apply existing models to new locations, to parameterize new models, or to parameterize existing models more specifically to account for changes in the physical environment or species.

We developed a species- and location-specific database of published ecophysiological variables typically used as input parameters for biogeochemical models of coniferous and deciduous forested ecosystems in the Western United States. We selected parameters based on the requirements of Biome-BGC (White et al. 2000), a widely used biogeochemical model that was originally parameterized for the forests of the Pacific Northwest. Biome-BGC is a daily time step, spatially independent model that simulates the development of soil and plant carbon and nitrogen pools by using 43 parameters (table 1). Although the input parameters for this database were investigated based on the structure of Biome-BGC, several other ecosystem models, including Century 5, Daycent, TEM, VEMAP (1995), and PnET (Aber et al. 1996), use some of the inputs described here.

The purpose of this database is to provide a compendium of ecophysiological data for the Pacific Northwest that will provide easily accessible information for particular tree species, parameters, and ecosystems for application to simulation modeling.

Methods

We used the databases Biosis and Agricola to conduct an extensive literature search for published ecophysiological data. We used the following keywords: Pacific Northwest, allocation, productivity, and ecophysiology. For species with few data, we used the common name and scientific name as keywords. Similarly, for parameters with few data, we searched by using keywords associated with that parameter specifically. We then used a "snowball" method by exploring the reference lists in sources with extensive literature citations. Finally we requested input from the University of Washington[1 2] and the University of Montana[3] for additional references. Occasionally, when important values were unavailable for a species in the Pacific Northwest, we included values for similar species from other regions and sometimes other continents.

[1]Hinckley, T. 2001, Personal communication. Professor, tree physiology, Center for Urban Horticulture, College of Forest Resources, University of Washington, Box 354115, Seattle, WA 98195-4115.

[2]Edmonds, R. 2001. Personal communication. Professor, forest soil microbiology and forest pathology, College of Forest Resources, University of Washington, Box 352100, Seattle, WA 98195-2100.

[3]Numerical Terradynamics Simulation Group. The University of Montana, College of Forestry and Conservation, Missoula, MT 59812.

Table 1—Input parameters and associated units required to run Biome-BGC[a]

Parameter description	Units
Woody or nonwoody	Flag
Evergreen or deciduous	Flag
C3 or C4 grass	Flag
Model-defined phenology or user-specified phenology	Flag
Yearday to start new growth (user-specified phenology)	Yrday
Yearday to end new growth (user-specified phenology)	Yrday
Transfer growth period as a fraction of growing season	Proportion
Litterfall as fraction of growing season	Proportion
Annual leaf and fine root turnover fraction	Proportion/yr
Annual live wood turnover fraction	Proportion/yr
Annual whole-plant mortality fraction	Proportion/yr
Annual fire mortality fraction	Proportion/yr
Allocation new fine root C:new leaf C	Ratio
Allocation new stem C:new leaf C	Ratio
Allocation new live wood C:new total wood C	Ratio
Allocation new root C:new stem C	Ratio
Allocation current growth	Proportion
C:N of leaves	kg C/kg N
C:N of leaf litter, after translocation	kg C/kg N
C:N of fine roots	kg C/kg N
C:N of live wood	kg C/kg N
C:N of dead wood	kg C/kg N
Leaf litter labile	DIM
Leaf litter cellulose	DIM
Leaf litter lignin	DIM
Fine root labile	DIM
Fine root cellulose	DIM
Fine root lignin	DIM
Dead wood cellulose	DIM
Dead lignin	DIM
Canopy water interception coefficient	1/LAId
Canopy light extinction coefficient	DIM
All-sided-area to projected-leaf-area ratio	DIM
Canopy average specific leaf area (projected area basis)	m^2/kg C
Shaded SLA:sunlit SLA	DIM
Fraction of leaf N in rubisco	DIM
Maximum stomatal conductance (projected area basis)	m/s
Cuticular conductance (projected area basis)	m/s
Boundary later conductance (projected area basis)	m/s
Leaf water potential:start of conductance reduction	MPa
Leaf water potential:complete conductance reduction	MPa
Vapor pressure deficit:start of conductance reduction	-Pa
Vapor pressure deficit:complete conductance reduction	-Pa

[a]Dimensionless values are denoted “DIM” .

If necessary, ecophysiological variables were converted to the International System of Units, and if possible, to the units used by Biome-BGC. We also recorded the species, location, elevation, and age (or time since disturbance) of the communities or populations studied whenever this information was available.

Parameter Definitions

One of the difficulties in developing a parameterization database that covers multiple species and vegetation types is that different methods may have been used to collect data relating to the same variable or parameter. Below we describe the typical definitions and methods for collecting measurements of each parameter. Note, however, that methods were not always consistent, and the individual studies should be referenced if methods are a concern.

Biomass and Productivity

Biomass is the mass of vegetation per unit area and is reported here in $kg \cdot m^{-2}$. Methods for determining aboveground biomass usually involve “clipping” all aboveground matter, drying it, and weighing it. Where belowground biomass is measured, roots are typically excavated, dried, and weighed.

Annual net primary productivity is the rate of carbon sequestered into dry matter per unit area over 1 year and is expressed here in $kg \cdot m^{-2} \cdot yr^{-1}$. Aboveground net primary productivity in forested ecosystems is measured in various ways, including allometric equations in which annual ring widths are used as indicators of annual volume increment or repeated measurements of stem diameter (Waring and Running 1998).

Allocation Parameters

Allocation relationships between different plant pools (carbon, nitrogen) control how carbon is allocated throughout the ecosystem or biome. Data for these allocation ratios were typically collected separately, for example, as fine root, coarse root, stem, and leaf. Note that live wood and dead wood have a particular connotation in Biome-BGC. Live wood includes the actively respiring woody tissue, i.e., the lateral sheathing meristem of phloem tissue, plus any ray parenchyma extending radially into the xylem tissue. Dead wood consists of all the other woody material, including the heartwood, xylem, and bark.

Carbon-to-Nitrogen Ratios

The mass ratio of carbon to nitrogen (C:N) in different plant components such as leaves, litter, roots, and live or dead wood is usually reported as the concentration of carbon divided by the concentration of nitrogen. If only the concentration of nitrogen is reported, the concentration of carbon is calculated from the dry weight of the plant component assuming that this is 50 percent carbon.

Decomposition Constant

The decomposition constant is based on an exponential pattern of loss and is calculated according to Olson (1963) based on litter bag loss, with the formula:

$$m_t/m_o = e^{-kt},$$

where m_t is the weight of the litter at time t, m_o is the initial weight of the litter, k is the decomposition constant and t is time. Solving for k, the decomposition constant is obtained as:

$$k = -ln(m_t/m_o)/t\ .$$

Efficiencies

Nutrient use efficiency is the proportion of organic matter produced for each unit of nutrient taken up. For long-lived plants, it is also a measure of how long a nutrient is retained in the plant to be used for carbon fixation.

Nitrogen and phosphorous use efficiency values are calculated here as the ratio of aboveground annual productivity to unit of nutrient uptake and are unitless. Two values are reported as dry mass·N litterfall^{-1}. Production use efficiency is defined as the proportion of aboveground net primary productivity relative to standing biomass.

Leaf Area Indices—Morphological Parameters

Leaf area index (LAI) is defined as the total leaf area on one surface of the leaf over a unit ground area and is expressed as $m^2 \cdot m^{-2}$. Specific leaf area (SLA) defines leaf area per unit of leaf carbon mass ($m^2 \cdot kg^{-1}$). Projected leaf area includes the leaf area projected horizontally on the ground surface, whereas all-sided leaf area includes the total surface area of leaves. The all-sided-area to projected-leaf-area ratio can be used to convert projected leaf area to all-sided leaf area, which is important for some physiological approximations such as canopy water interception (Barclay 1998). The LAI can be measured with a wide range of techniques including radiation transmittance (Chen et al. 1997), sapwood allometrics (Sampson and Smith 1993), and foliage biomass.

The canopy light extinction coefficient is the Beer's law extinction coefficient, which controls the attenuation of radiation from the top of the canopy to the ground owing to leaf absorption and reflection. Canopy light extinction coefficients are typically estimated with a radiation measuring device such as a sunfleck ceptometer.

Nitrogen Distribution

Nitrogen distribution among the different biomass components (aboveground, belowground, litter, and forest floor) is determined by chemical analysis of samples by using standard procedures and is expressed as kg $N \cdot m^{-2}$. Soil nitrogen is usually determined separately for each horizon, and the total value is reported here as kg $N \cdot m^{-2}$.

Nitrogen Input

Nitrogen input represents an estimate of atmospheric nitrogen deposition, usually through precipitation or dust. The value is reported in kg $N \cdot m^{-2}$.

Carbon Proportions: Labile, Cellulose, Lignin

Typically, lab techniques are used to determine proportions of carbon allocated to each class (labile, cellulose, or lignin) (White et al. 2000). Labile pools include the easily decomposed fractions, such as carbohydrates that are soluble in hot water and alcohol. Cellulose is the fraction soluble in an acid bath, after extraction of the labile fraction. The remainder is calculated as the lignin pool. The labile, cellulose, and lignin fractions must sum to 1.

Leaf and Fine Root Turnover

Turnover refers to the proportion of the carbon pool replaced each year and is the inverse of the mean residence time (White et al. 2000). For deciduous species, leaf and fine root turnover is set to 1. For evergreen trees, turnover is calculated as the inverse of leaf longevity.

We did not include data for all the ecophysiological variables needed to parameterize Biome-BGC in the database either because they do not change significantly among biomes or because data are extremely sparse, and we were not able to find them for tree species of the Pacific Northwest. For these variables, refer to White et al. (2000).

Results

The literature search yielded ecophysiological information for 18 evergreen needleleaf, 2 deciduous broadleaf, and 2 deciduous needleleaf tree taxa common in the Pacific Northwest (table 2). Species-specific data on 37 variables (table 3), including 587 values critical for model parameterization, are recorded in a Microsoft Access®[4] relational database.

[4]The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

Table 2—Species code, scientific name, and common name of tree species included in the database[a]

Species code	Scientific name	Common name
ABAM	*Abies amabilis* Dougl. ex Forbes	Pacific silver fir
ABCO	*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.	White fir
ABGR	*Abies grandis* (Dougl. ex D. Don) Lindl.	Grand fir
ABLA	*Abies lasiocarpa* (Hook.) Nutt.	Subalpine fir
ABPR	*Abies procera* Rehd.	Noble fir
ALRU	*Alnus rubra* Bong.	Red alder
JUOC	*Juniperus occidentalis* Hook.	Western juniper
LALY	*Larix lyallii* Parl.	Alpine larch
LAOC	*Larix occidentalis* Nutt.	Western larch
LIDE	*Libocedrus decurrens* Torr.	Incense-cedar
PIEN	*Picea engelmannii* Parry ex Engelm.	Engelmann spruce
PISI	*Picea sitchensis* (Bong.) Carr.	Sitka spruce
PIAL	*Pinus albicaulus* Engelm.	Whitebark pine
PICO	*Pinus contorta* Dougl. ex Loud.	Lodgepole pine
PILA	*Pinus lambertiana* Dougl.	Sugar pine
PIPO	*Pinus ponderosa* Dougl. ex Loud.	Ponderosa pine
POTR	*Populus tremuloides* Michx.	Quaking aspen
PSME	*Pseudotsuga menziesii* (Mirb.) Franco	Douglas-fir
TABR	*Taxus brevifolia* Nutt.	Pacific yew
THPL	*Thuja plicata* Donn ex D. Don	Western redcedar
TSHE	*Tsuga heterophylla* (Raf.) Sarg.	Western hemlock
TSME	*Tsuga mertensiana* (Bong.) Carr.	Mountain hemlock

[a]Species authorities not included in the database.

With the exception of leaf area parameters (evergreen needleleaf) and C:N ratio of dead wood (deciduous broadleaf), all the mean parameter values for each leaf type are within one standard deviation of those reported elsewhere (White et al. 2000) (tables 4, 5, 6, 7, and 8). For example, we report a mean of 0.26 (SD = 0.10, n = 50) for leaf and fine root turnover for evergreen needleleaf trees of the Pacific Northwest. This compares with a mean of 0.26 (SD 0.15, n = 129) for evergreen needleleaf species from other temperate regions (White et al. 2000).

Mean values for leaf characteristics described here highlight critical differences between the evergreen needleleaf forests of the Pacific Northwest and those studied elsewhere. For example, mean SLA for evergreen needleleaf trees of the Pacific Northwest is much higher and more variable (mean = 20.66, SD = 15.01, n = 24) (table 8) than reported for evergreen needleleaf trees from other regions (White et al. 2000 report mean = 8.2, SD = 3.6, n = 39). Species-level means indicate that several species (especially *Tsuga heterophylla*, *Abies amabilis*, *Pseudotsuga menziesii*, and *A. procera*) occurring in low- to mid-elevation west-side environments

Table 3—Ecophysiological variables and their associated units included in the database[a]

Parameter	Units
Biomass—aboveground	$kg \cdot m^{-2}$
Biomass—belowground	$kg \cdot m^{-2}$
Biomass—total	$kg \cdot m^{-2}$
Productivity—aboveground NPP	$kg \cdot m^{-2} \cdot yr^{-1}$
Productivity—belowground NPP	$kg \cdot m^{-2} \cdot yr^{-1}$
Productivity—total NPP	$kg \cdot m^{-2} \cdot yr^{-1}$
Carbon allocation—coarse root C:stem C	DIM
Carbon allocation—new fine root C:new leaf C	DIM
Carbon allocation—new live wood C:new total wood C	DIM
Carbon allocation—new stem C:new leaf C	DIM
C:N ratio—dead wood	kg C/kg N
C:N ratio—fine root	kg C/kg N
C:N ratio—leaf	kg C/kg N
C:N ratio—litter	kg C/kg N
Decomposition—annual constant	DIM
Efficiency—nitrogen—use	kg ANPP/kg N/yr[b]
Efficiency—phosphorous—use	kg drymass/kg litterfall N
Leaf area—all sided:projected	$m \cdot m^{-2}$
Leaf area index	$m \cdot m^{-2}$
Leaf area—light extinction coefficient	DIM
Leaf area—specific	$m^{2} \cdot kg^{-1}$ C
Nitrogen—aboveground	$kg \cdot m^{-2}$
Nitrogen—belowground	$kg \cdot m^{-2}$
Nitrogen—forest floor	$kg \cdot m^{-2}$ [c]
Nitrogen—input	$kg \cdot m^{-2} \cdot yr^{-1}$
Nitrogen—litter	$kg \cdot m^{-2} \cdot yr^{-1}$
Nitrogen—soil	$kg \cdot m^{-2}$
Proportion—dead wood—cellulose	DIM
Proportion—dead wood—labile	DIM
Proportion—dead wood—lignin	DIM
Proportion—fine root—cellulose	DIM
Proportion—fine root—labile	DIM
Proportion—fine root—lignin	DIM
Proportion—litter—cellulose	DIM
Proportion—litter—labile	DIM
Proportion—litter—lignin	DIM
Proportion—annual turnover—leaf and root	1/yr

[a]Dimensionless values are denoted "DIM".

[b]Two values are recorded as drymass/litter fall N.

[c]Three values are recorded as $kg \cdot m^{-2} \cdot yr^{-1}$.

Table 4—Biomass of forest stands in this database

Leaf type	Biomass	Mean	Minimum	Maximum	SD	N
		Kilograms per square meter				
Deciduous broadleaf	Total	21.00	21.00	21.00	NA	1
	Aboveground	14.73	7.80	24.00	6.17	6
	Belowground	3.46	1.08	5.80	2.36	3
Evergreen needleleaf	Total	66.89	7.60	117.00	34.92	12
	Aboveground	45.67	2.00	149.20	35.27	46
	Belowground	22.58	3.30	80.60	27.91	17

NA = not applicable.

Table 5—Net primary productivity (NPP) of forest stands in this database

Leaf type	Productivity	Mean	Minimum	Maximum	SD	N
		Kilograms per square meter per year				
Deciduous broadleaf	Total NPP	1.71	1.46	1.95	.35	2
	Aboveground NPP	1.35	1.03	1.70	.34	3
	Belowground NPP	.17	.12	.24	.06	3
Deciduous needleleaf	Aboveground NPP	.10	.10	.10	NA	1
Evergreen needleleaf	Total NPP	1.58	.79	3.62	.96	7
	Aboveground NPP	1.47	.12	10.5	2.12	44
	Belowground NPP	.50	.20	1.22	.28	20

NA = Not applicable.

Table 6—Carbon allocation ratios of forest stands in this database

Leaf type	Carbon allocation	Mean	Minimum	Maximum	SD	N
Deciduous broadleaf	Coarse root C:stem C	.21	.15	.27	.09	2
	New live wood C:new total wood C	.10	.10	.10	NA	1
	New stem C:new leaf C	2.40	1.69	3.07	.56	6
Deciduous needleleaf	New live wood C:new total wood C	.10	.10	.10	NA	1
Evergreen needleleaf	Coarse root C:stem C	.27	.19	.44	.07	10
	New fine root C:new leaf C	2.89	.67	10.81	2.71	14
	New live wood C:new total wood C	.07	.06	.07	.01	2
	New stem C:new leaf C	1.92	.20	3.32	.86	36

NA = not applicable.

contribute to this high mean (table 9). Based on recent work, differences in SLA may be critical for modeling productivity (Reich et al. 1999, White et al. 2000). As a result, these input parameters should be defined with close attention to variability within and among species.

We found data about mean C:N for dead wood for only two deciduous broadleaf species of Pacific Northwest trees, i.e., *Populus tremuloides* and *Alnus rubra*.

Table 7—Plant component ratio of forest stands in this database

Leaf type	Plant component	Mean	Minimum	Maximum	SD	N
Deciduous broadleaf	Dead wood	149.35	107.30	196.00	41.01	4
	Fine root	56.80	56.80	56.80	NA	1
	Leaf	22.56	18.40	29.40	3.80	7
	Litter	49.65	23.80	80.00	22.71	7
Deciduous needleleaf	Dead wood	270.00	270.00	270.00	NA	1
	Leaf	29.12	24.40	35.00	4.50	5
Evergreen needleleaf	Dead wood	854.71	139.00	1400.00	335.50	14
	Fine root	67.37	48.00	90.90	17.34	7
	Leaf	46.06	35.70	75.80	9.21	16
	Litter	85.09	49.20	135.00	23.23	18

NA = not applicable.

Table 8—Leaf area parameters of forest stands in this database

Leaf type	Leaf area	Mean	Minimum	Maximum	SD	N
Deciduous broadleaf	Leaf area index	4.45	2.50	6.40	2.76	2
	Specific leaf area ($m^2 \cdot kg^{-1}$)	35.40	24.20	46.60	15.84	2
Deciduous needleleaf	Specific leaf area ($m^2 \cdot kg^{-1}$)	21.04	15.20	26.36	4.81	5
Evergreen needleleaf	All-sided: projected leaf area	2.42	2.32	2.57	.08	7
	Leaf area index	14.46	2.00	46.43	12.35	14
	Specific leaf area ($m^2 \cdot kg^{-1}$)	20.66	2.08	42.26	15.01	24

NA = not applicable.

Table 9—Evergreen needleleaf species with reported mean specific leaf areas >25.0

Species	Mean	Minimum	Maximum	SD	N
	Square meters of leaf per kilogram carbon				
Tsuga heterophylla	35.88	21.00	42.26	8.12	6
Abies amabilis	30.40	30.40	30.40	NA	1
Pseudotsuga menziesii	26.67	8.94	38.88	13.83	6
Abies procera	26.38	26.38	26.38	NA	1

NA = not applicable.

Their dead wood C:N ratio was much lower than for deciduous trees in other regions, indicating a larger availability of nitrogen for microbial decomposition. These higher nitrogen values suggest that dead wood will decompose quickly and will provide more nitrogen to be cycled in the system relative to other deciduous forests.

Although mean ecophysiological parameters for Pacific Northwest trees may be similar to the mean values for trees of the same leaf type from other regions, there is great variability among species and location. For example, total biomass (aboveground and belowground) for evergreen needleleaf forests ranged between 7.6 kg·m^{-2} for *Abies amabilis* at Findley Lake, Washington (Vogt et al. 1982), and 117 kg·m^{-2} for *Pseudotsuga menziesii* at the H.J. Andrews Forest, Oregon (Grier and Logan 1977). Similarly, aboveground annual productivity ranges between 0.10 kg·m^{-2}·yr^{-1} for *Larix occidentalis* on Chumstick Mountain, Washington (Gower et al. 1989), and 10.5 kg·m^{-2}·yr^{-1} for *P. menziesii* in the interior Coast Range of Oregon (Gholz 1982). For *P. menziesii* alone, aboveground productivity ranges between 0.51 kg·m^{-2}·yr^{-1} for the Thompson Research Center, Washington (Turner and Long 1975), and the aforementioned 10.5 kg·m^{-2}·yr^{-1} in the interior Coast Range, Oregon. This extreme variation suggests careful application of mean parameter values in topographically and biologically diverse regions like the Pacific Northwest.

Our results also point to a number of serious deficiencies in empirical data. We did not locate any references describing leaf nitrogen in rubisco, the key enzyme leading to photosynthesis that is one of the more sensitive parameters used in Biome-BGC (White et al. 2000). In addition, few data exist on high-elevation species such as *Larix lyallii* (three values), *Pinus albicaulis* (two values), and *Tsuga mertensiana* (eight values).

Conclusions

Our results suggest that morphological parameters critical for model input are available for most major tree species in the Pacific Northwest and should be carefully defined in simulation models. In addition, the variability of parameters within and between species indicates a need to consider location and species composition in model runs when possible.

We hope these data will motivate additional modeling, empirical data collection, laboratory analysis, and database development in the Pacific Northwest and in other regions. Although some Pacific Northwest species (e.g., *Pseudotsuga menziesii*) and some ecophysiological parameters (e.g., aboveground biomass) have been studied extensively, others have only a few references for a few species (e.g., decomposition constant). The database of parameters has deficiencies in the following areas: percentage of leaf nitrogen in rubisco (no data listed here), decomposition constants for most species, nitrogen use efficiencies for most species, and data on most parameters for subalpine species. We hope that additional data collection in these areas will supplement existing knowledge. It is the careful collection of field and laboratory data that allows scientists to parameterize and validate ecosystem models at all scales, from local ecosystem models to global biogeochemical models.

Acknowledgments

We thank Paige Eagle for developing the relational database included in a CD-ROM attached to this report.

English Equivalents

When you know:	Multiply by:	To find:
Kilograms per square meter ($kg \cdot m^{-2}$)	0.20	Pounds per square foot
Square meters (m^2)	10.76	Square feet
Square meters per kilogram ($m^2 \cdot kg^{-1}$)	4.95	Square feet per pound
Milligrams per gram ($mg \cdot g^{-1}$)	1,000	Parts per million
Mega Pascal (Mpa)	20,900	Pounds per square foot
Pascal (Pa)	.0209	Pounds per square foot
Meters per second ($m \cdot s^{-1}$)	3.28	Feet per second

Literature Cited

Aber, J.D. 1997. Why don't we believe the models? Bulletin of the Ecological Society of America. 78: 232–233.

Aber, J.; Reich, P.B.; Goulden, M.L. 1996. Extrapolating leaf CO_2 exchange to the canopy: a generalized model of forest photosynthesis compared with measurements by eddy correlation. Oecologia. 106: 257–265.

Barclay, H. 1998. Conversion of total leaf area to projected leaf area in lodgepole pine and Douglas-fir. Tree Physiology. 18: 185–193.

Chen, J.M.; Blanken, P.D.; Black, T.A.; Guibeault, M.; Chen, S. 1997. Radiation regime and canopy architecture in a boreal aspen forest. Agricultural and Forest Meteorology. 86: 107–125.

Gholz, H. 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. Ecology. 63: 469–481.

Gower, S.; Grier, C.; Vogt, K.A. 1989. Aboveground production and N and P use by *Larix occidentalis* and *Pinus contorta* in the Washington Cascades, USA. Tree Physiology. 5: 1–11.

Grier, C.; Logan, R. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. Ecological Monographs. 47: 373–400.

Neilson, R.P. 1995. A model for predicting continental-scale vegetation distribution and water balance. Ecological Applications. 5: 362–385.

Olson, J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology. 44: 322–331.

Reich, P.B.; Ellsworth, D.S.; Walters, M.B.; Vose, J.M.; Gresham, C.; Volin, J.C.; Bowman, W.D. 1999. Generality of leaf trait relationships: a test across six biomes. Ecology. 80: 1955–1969.

Running, S.W. 1994. Testing forest-BGC ecosystem process simulations across a climatic gradient in Oregon. Ecological Applications. 4: 238–247.

Sampson, D.; Smith, F. 1993. Influence of canopy architecture on light penetration in lodgepole pine (*Pinus contorta* var. *latifolia*) forests. Agricultural and Forest Meteorology. 64: 63–79.

Turner, J.; Long, J. 1975. Accumulation of organic matter in a series of Douglas-fir stands. Canadian Journal of Forest Research. 5: 681–690.

Vegetation Ecosystem Modeling and Analysis Project [VEMAP]. 1995. Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO_2 doubling. Global Biogeochemical Cycles. 9: 407–437.

Vogt, K.; Grier, C.; Meier, C.E.; Edmonds, R.L. 1982. Mycorrhizal role in net primary production and nutrient cycling in *Abies amabilis* ecosystems in western Washington. Ecology. 63: 370–380.

Waring, R.H. 1993. How ecophysiologists can help scale from leaves to landscapes. In: Ehleringer, J.R.; Field, C.B., eds. Scaling physiological processes: leaf to globe. San Diego, CA: Academic Press: 159–166.

Waring, R.H.; Running, S.W. 1998. Forest ecosystems: analysis at multiple scales. San Diego, CA: Academic Press. 370 p.

White, M.A.; Thornton, P.E.; Running, S.W.; Nemani, R.R. 2000. Parameterization and sensitivity analysis of the Biome-BGC terrestrial ecosystem model: net primary productivity controls. Earth Interactions. 4: 1–85.

Appendix A: Instructions

Microsoft Access® Users

One search form, built into the database, allows users to search for all data by species, parameter, and location, then allows users to view and print the parameter values and citations to a file. This file can be printed as text or downloaded to other applications (Microsoft Excel®). The data also can be accessed as a series of text files that can be used with a variety of applications. Advanced Microsoft Access® users may wish to forgo the search form and create their own queries on the database by using Microsoft Access® query tools.

Text or Other Database Users

Seven comma-delimited text files also have been included on the CD-ROM attached to this publication to allow researchers who are using software other than Microsoft Access® to use the database. These files are entitled:

- Parameters.txt—includes a list of parameters and definitions
- Parameter-Location.txt—links parameters with locations
- Parameter-Species.txt—links parameters with species
- ParameterValues.txt—includes parameter values, species, site, and reference information (this is the critical table)
- References.txt—includes the list of references for the parameter values
- Species.txt—defines the species, scientific name, four-letter acronym, and common name for all species included
- Location.txt—defines the abbreviation for place names used in ParameterValues

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