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Sources of variation in ecophysiological parameters in Douglas-fir and grand fir canopies

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Summary Forest process models predict ecosystem responses from climate variables and physiological parameters. The parameters describe key ecosystem attributes, often as lumped averages. However, the sources and magnitude of variation in these physiological parameters are unknown, which complicates sampling if models are to be parameterized with field measurements. We measured several key parameters, which had been identified by sensitivity analyses of three models, in *Abies grandis* (Dougl.) Lindl. and *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco trees throughout the growing season. Trees were sampled at eight sites across the interior northwest of the USA. At each site, fertilized and control plots were sampled. The design provided statistical replication for the analysis of variance within a site, allowing us to draw inferences about a regional population of stands. Specific leaf area (SLA) varied by canopy position and treatment ($P = 0.0003$), by date of sampling ($P < 0.0001$) and by species ($P = 0.0188$). Mass-based foliar nitrogen concentration (%N) increased during the summer in both species ($P = 0.0019$), but at a faster rate in *P. menziesii* var. *glauca* than in *A. grandis*. Sun foliage had a higher mean %N (1.00, SE = 0.02%) than shade foliage (0.92 ± 0.01%). Apparent quantum yield (Φ) varied among treatments, between species and between canopy positions; each of these variables interacted with date of sampling ($P = 0.0207$, $P < 0.0001$ and $P = 0.0344$, respectively). In *A. grandis*, mean Φ values (± SE) were 0.048 ± 0.006 mol CO_2 (mol incident photon)$^{-1}$ for sun foliage and 0.067 ± 0.007 mol CO_2 (mol incident photon)$^{-1}$ for shade foliage. In *P. menziesii*, the corresponding mean Φ values were 0.032 ± 0.003 and 0.047 ± 0.004 mol CO_2 (mol incident photon)$^{-1}$. Parameters SLA, %N and Φ were all influenced by date, fertilizer treatment, species and crown position. We discuss methods of inferring quantum yields from light response curves and their utility for parameterizing process models. Parameter mean values are presented for each site; these tables provide a documented data set for the parameterization of models describing the western interior forests of the USA.

Keywords: Abies grandis, foliar nitrogen concentration, process models, Pseudotsuga menziesii var. glauca, quantum yield, sensitivity analyses, specific leaf area.

Introduction

Process models have been successfully used to predict large-scale phenomena, such as biomass production and atmospheric gas transport, from physiological processes regulating forest growth at the cellular level (Landsberg and Gower 1997, Waring and McDowell 2002). To make it possible to parameterize such models, they are based on simplifying assumptions. In many models, this simplification is achieved by bulking or lumping subunits of the system and then using a single parameter to describe the lumped subunit (Running and Coughlan 1988, Running and Gower 1991, Aber and Federer 1992, Landsberg and Waring 1997, Waring and Running 1998). Examples of lumped parameters used to describe forest canopies include quantum efficiency, foliar mass-to-area ratio and nitrogen (N) concentration.

The use of lumped parameters leads to questions about how the lumped parameters are to be measured. Ideally, measurements made at a particular time and position can be used to describe the canopy as a whole (Wallin et al. 2001). Parameter measurements are averaged across the canopy, and the mean may be weighted by relative fluxes (Jarvis 1995). However, many important leaf parameters vary two- to fivefold with canopy position (Bond et al. 1999) and by similar amounts among co-occurring species (Bassow and Bazzaz 1997), so it can be difficult to obtain accurate estimates of mean values of canopy parameters (Jarvis 1995).

Some parameters vary such that correlations among the parameters are maintained. These correlations provide opportunities to make a simple measurement to infer a more difficult one. For example, specific leaf area and foliar N concentration vary considerably with canopy position, but they are correlated throughout their respective ranges (Reich et al. 1991, 1997).

The current study was motivated by the need to estimate lumped parameters for a modeling exercise. Our overall plan is to parameterize several common, highly simplified models of forest biogeochemistry in an effort to explain observed changes in forest growth following fertilization across a large swathe of the northern Rocky Mountains in western USA. In this study, we focused on quantifying the variation in parameters identified by sensitivity analyses of Forest-BGC (Running and Coughlan 1988, Running and Gower 1991), PnET (Aber and Federer 1992) and 3-PG (Landsberg and Waring 1997). The sensitivity analysis identified a small number of influential lumped parameters, including specific leaf area, photosynthetic quantum yield, foliar N concentration and maximum photosynthetic rate (Aber et al. 1996, Battaglia and Sands 1998, White et al. 2000).

We used mixed-effects models analysis of variance to analyze the sources of variation in the lumped parameters at eight sites between the Cascade and Rocky Mountain crests in northwestern USA. At each site, we measured foliage from the top and bottom of the canopy to account for spatial variation, compared treatments from a region-wide fertilization experiment to account for nutrient variation, performed measurements throughout the growing season to account for temporal variation, and compared two species belonging to different genera to account for interspecific variation. Given the difficulty of explaining how the data were collected and analyzed, running the models with the range of observed variation in the parameters is beyond the scope of the current paper. Our goal in this study was to evaluate a method for measuring model parameters and to analyze the sources of parameter variation within the forest canopy. We present the results of our analyses by site, to allow the modeling community to use them for parameterization, but also as a first step in the assessment of the generality of the simplifying assumptions embedded in current models.

Materials and methods

Site selection and sampling

During 1994–1996, the Intermountain Forest Tree Nutrition Cooperative (IFTNC) at the University of Idaho established a replicated fertilization study throughout the interior northwest of the USA (Garrison et al. 1997). We chose eight sites with a basaltic parent material out of the 31 possible sites. These eight sites varied by vegetation series, aspect, elevation, basal area, relative density and tree height (Table 1, Figure 1). Four fertilization treatments were applied at each site, including N only (336 kg ha^{-1}), potassium (K) only (224 kg ha^{-1}), N + K (336 + 224 kg ha^{-1}) and an unfertilized control. We measured two species varying in shade tolerance within each fertilizer treatment: Rocky-mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), which is intermediate in shade-tolerance, and grand fir (*Abies grandis* (Dougl.) Lindl.), a more shade-tolerant species. Sun and shade foliage was sampled from 1-year-old needles from one tree per species and treatment combination. Foliage samples were harvested by tree-climbing. Sun foliage was selected from the exposed upper crown (second to sixth whorl from the top) and shade foliage was harvested from the lowest live whorl. Samples were collected three times: May 28–June 21, June 27–July 14 and September 10–22, 2001. These sampling periods (hereafter designated June, July and September) represent the period of leaf elongation, the beginning of the rainless period and the peak of summer drought, respectively.

Table 1. Characteristics of the study sites. Vegetation series refers to the classification of forest communities into habitat types based on the potential climax vegetation present (Daubenmire and Daubenmire 1968). Abbreviations: TSHE = *Tsuga heterophylla* (Rafn.) Sarg.; THPL = *Thuja plicata* Donn; ABGR = *Abies grandis*; and PSME = *Pseudotsuga menziesii* var. *glauca*. Relative density index is the degree of stocking within a stand expressed as a ratio of the mean maximum area per tree relative to the observed area (Curtis 1982). Mean precipitation and mean maximum temperatures were calculated based on Daymet climatological summaries (www.daymet.org).

Map number	Site name	Location	Latitude/ longitude	Vegetation series	Site aspect	Elevation (m)	Live basal area	Relative density index	Mean tree height	Mean precipitation (cm year^{-1})	Mean max. temperature (°C year^{-1})
1	Soldier Creek	Northern Idaho	47°20′ N 116°45′ W	TSHE	202°	976	34.4	51	19.8	101.6	13.2
2	Sportsman's Access	Northern Idaho	47°23′ N 116°53′ W	TSHE	337°	945.5	18.8	27	23.8	97.4	13.4
3	Dick's Creek	Northern Idaho	46°29′ N 116°15′ W	THPL	0°	915	37.8	55	24.4	70.3	15.5
4	Upper Pataha #2	Southeastern Washington	46°29′ N 117°36′ W	ABGR	45°	1525	6.2	12	7.3	56.9	14.4
5	Enterprise	Northeastern Oregon	45°26′ N 117°17′ W	PSME	247°	1433.5	26.4	37	21.4	111.6	6.6
6	Cleman Mountain #2	Central Washington	46°44′ N 120°42′ W	PSME	180°	1037	26.4	32	21.7	22.4	17.7
7	BZ Corner #2	South-central Washington	45°99′ N 121°29′ W	ABGR	112°	579.5	64.2	70	37.2	143.0	14.1
8	Snowden Mountain #2	South-central Washington	45°75′ N 121°45′ W	PSME	0°	671	33.3	40	29	116.8	14.6

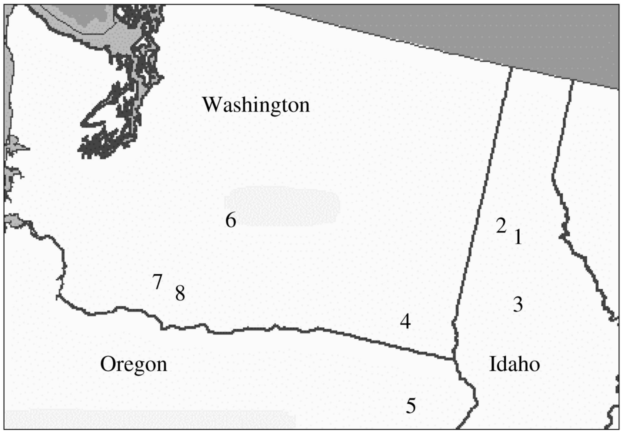

Figure 1. Map of the study region comprising the interior northwest of the USA. Each number corresponds to a study site listed in Table 1.

Gas exchange measurements

We measured assimilation on excised foliage with a Li-Cor LI-6400 portable photosynthesis system with a red/blue LED light source and CO_2 injector (Li-Cor, Lincoln, NE). The instrument was zeroed and chemicals were replaced daily. The instrument was less than 6 months old so the factory calibration was considered reliable (Li-Cor 6400 manual). Measurements were performed at intervals during the course of the day. The temperature within the cuvette was maintained near ambient, that is, between 19 and 23 °C. Cuvette CO_2 concentrations ranged between 385 and 395 µmol mol^{-1}. A fixed airflow of 500 µmol s^{-1} was maintained during measurements, and the relative humidity inside the cuvette ranged between 5 and 20%.

We determined that grand fir and Douglas-fir foliage maintained constant CO_2 assimilation rates for 50 min following excision. Therefore, measurements never exceeded 35 min from the time of excision. Following collection, we placed the foliage inside the cuvette to acclimate. Once net CO_2 assimilation had stabilized (coefficient of variation less than 10%), gas exchange measurements were performed. Light-response curves were generated by decreasing photosynthetically active radiation (PAR) from 1500 to 750, 250, 75, 30, 10 and 0 µmol m^{-2} s^{-1}. We made four measurements at PAR < 100 µmol m^{-2} s^{-1} to improve our estimates of quantum yield (Singsaas et al. 2001). Leaves were allowed to acclimate for 2 to 4 min before each measurement. Foliage samples were stored over ice in airtight containers until they were returned to the laboratory and stored at –70 °C.

Gas exchange measurements were expressed as projected area of the foliage within the cuvette (Leverenz et al. 2000). Leaf area images were generated by scanning needles at a resolution of 200 dpi and the projected areas were determined with image analysis software (SigmaScan Pro 5.0, SPSS Science, Chicago, IL, 1999). To determine the accuracy of estimating leaf area with the imaging software, we measured a subset of the foliage with precision calipers to the nearest 0.1 mm. Estimates by the two methods varied by less than 8%, and there was no consistent bias.

Specific leaf area

To estimate specific leaf area (SLA), we scanned about 30–40 needles positioned with the adaxial side down. Following leaf area analysis, samples were dried at 70 °C for 72 h and weighed.

Foliar percent nitrogen

The foliage samples measured for gas exchange were ground to a fine homogeneous texture and processed with an elemental analyzer combined with continuous-flow isotope ratio mass spectrometry to determine elemental composition. Foliar percent nitrogen (%N) was calculated as the mass (mg) of nitrogen per total mass of the sample (mg) multiplied by 100. All %N values were verified relative to working standards of known N concentration dispersed throughout the analysis.

Fitting light-response curves

The photosynthetic light response has been described by several equations. We fitted three forms by nonlinear least squares regression to determine which best described our data (Landsberg and Gower 1997, Bond et al. 1999, Whitehead and Gower 2001). Nonlinear curve fitting has the advantage of simultaneously fitting all the coefficients in the model. Thus the curvature in the line is accounted for, allowing the fit to assign the highest possible value to the initial slope that is consistent with least squares constraint. Because this approach is both objective and provides the best possible fit, it is a substantial improvement over fitting a straight line to a subjectively chosen number of points along the curve (Singsaas et al. 2001).

After fitting our data to the models, we compared the fit of all three equations using Akaike's information criterion. In addition, we compared the slope of the light-response curve at PAR = 0 to the slope of a line passing through the light compensation point ($A = 0$). Specifically, we looked for a 1:1 ratio based on the assumption that the apparent Kok effect (Kirschbaum and Farquhar 1987) should have little influence (< 10%) over this range of PAR. The slope at $A = 0$ describes the leaf at a known intercellular CO_2 concentration (c_i). Because $A = 0$, c_i must be equal to ambient CO_2 concentration (c_a) at this point. The concentration at PAR = 0 would be substantially higher but by an unknown amount. Because it is difficult to measure c_i at the low stomatal conductances that occur in the linear portion of the light-response curve, we concluded that $A = 0$ provided the best reference point.

We also compared R^2 values to determine which model had the best fit. An example light curve, chosen at random, is presented in Figure 2A, and shows that the model selected describes the general form of the data well. Additionally, examination of the lowest PAR values (Figure 2B) shows how the model estimates quantum yield at the light compensation point, expressed as a linear relationship, compared with the overall nonlinear model fit. Based on the statistical comparisons and theoretical considerations mentioned previously, we chose the non-rectangular hyperbolic model developed by Hanson et al. (1987) and used it to derive estimates of quantum yield (Φ), light compensation point (Γ), maximum assimila-

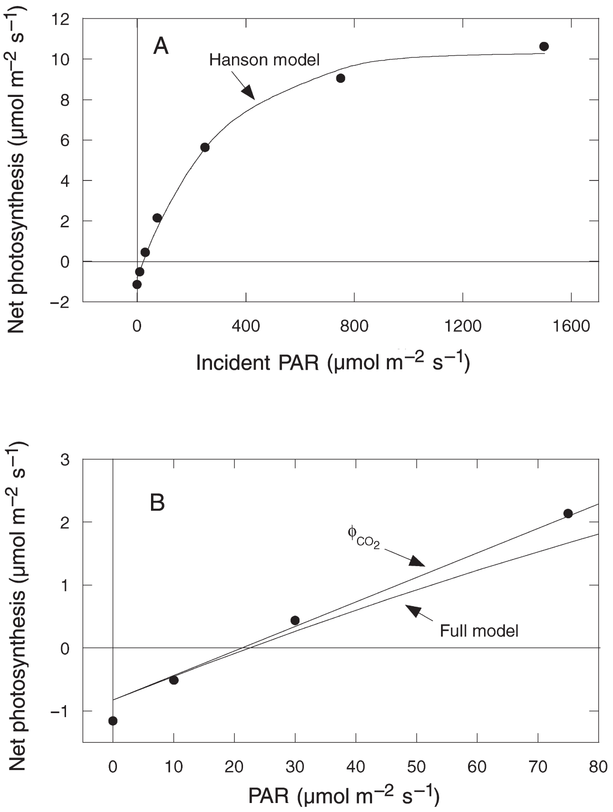

Figure 2. (A) Light response data for a randomly chosen sun branch. The solid line shows the curve fitted by nonlinear regression to the model form selected for this study (Hanson et al. 1987). (B) Subset of the data in Figure 2A, focusing on the lowermost photosynthetically active radiation (PAR) values. In addition to the curved line showing the complete model fit, the quantum yield estimates are presented as straight lines. The Hanson et al. (1987) model was used to estimate the slope at $A = 0$ (light compensation point).

tion rate (A_{max}) and dark respiration rate (R_d):

$$A = A_{max}\left(1-\left(1-\frac{R_d}{A_{max}}\right)^{(1\,-\,\mathrm{PAR}/\Gamma)}\right) \tag{1}$$

We derived estimates of A_{max}, Φ and R_d from Equation 1. From these estimates, we derived apparent quantum yield as the first derivative when PAR = 0 (at R_d) with Equation 2.

$$\Phi = \left(\frac{A_{max}}{\Gamma}\right)\left(1-\frac{R_d}{A_{max}}\right)\ln\left(1-\frac{R_d}{A_{max}}\right) \tag{2}$$

Three hundred and forty-one light-response curves were fitted by the nls procedure of S-PLUS 2000 (Mathsoft, Cambridge, MA). Following curve development, 11 outliers were removed because their calculated values lay above the theoretical maximum quantum efficiency rate of 0.125 mol C (mol incident photon)$^{-1}$ (Björkman and Demmig 1987).

Statistical analysis

Linear mixed-effects models were developed to determine the statistical significance of the predictor (independent) variables on the response (dependent) variables of interest. In model development, each response variable was fit as a unique function of multiple fixed and random effects. Each model incorporated the grouped structure of a repeated measures split-plot design of species within treatments within sites. Sites were used as replicates to characterize this region. In the analysis, sites were a randomly assigned blocking variable. We chose to block this study to reduce the error variance and isolate site differences as nuisance variables. By reducing the nuisance variation, blocking allows for a more precise estimate of significant predictor variables. The geographic range included in this study provided true replication and allowed us to draw inferences about sources of variation across the entire region.

During model development, all of the response variables were transformed to satisfy model assumptions. The assumptions included independence of within-group errors and random effects, constant variance, and normally distributed residuals and random effects (Pinheiro and Bates 2000). Henceforth, transformed results are reported, unless the transformation did not change the significance of the results (Table 2). Unless otherwise stated, significance refers to $P < 0.05$. All model development and analysis was performed with the lme function of S-PLUS 2000 (Mathsoft). Pairwise comparisons of all treatment means were performed using the Tukey Honestly Significant Difference (HSD) procedure. The HSD was calculated from the mean-squared error from the full model. An effect was considered significant when the 95% simultaneous-confidence-interval estimate was exceeded.

Results

The SLA of the 1-year-old foliage changed as current-year canopy foliage expanded and matured over the summer. Values of SLA increased significantly in each summer sampling period; there was a 10 and 26% increase during the June–July and June–September periods, respectively (Figure 3). Fertilizer effects on SLA depended on canopy position (Figure 4). In shade foliage, SLA was lower in K-treated trees than in N + K-treated trees. However, in sun foliage, SLA was lower in N-treated trees than in N + K-treated trees.

Foliar %N values also varied in the forests we measured. Sun foliage had a higher mean (± SE) %N (1.00 ± 0.02%) compared with shade foliage (0.92 ± 0.01%). The %N also varied by species and sample date (Figure 5). Douglas-fir had a greater %N than grand fir in June and September. The difference in %N between species increased by 5 to 12% during the summer. Likewise, the increase in %N from June to September was twice as high in Douglas-fir (17%) as in grand fir (8%).

Apparent quantum yield varied by species, summer period, canopy position and fertilizer treatment. Shade foliage had a higher mean Φ than sun foliage for each summer period (Figure 6A). In June, the difference in Φ between canopy positions

Table 2. Summary of the mixed-effects model analysis of variance. Unless noted, response variables did not require transformations to satisfy model assumptions. Interactions between predictor variables are listed for each response variable only if significant ($P < 0.05$). Blank cells indicate a nonsignificant interaction. Abbreviations: SLA = specific leaf area; %N = foliar percent nitrogen; Φ = quantum yield; $A_{\max}$ = maximum assimilation; R_d = dark respiration; and Γ = light compensation point.

Predictor variables	Response variables					
	SLA	%N	Φ	log ($A_{\max}$)	R_d	$\log(\Gamma)^2$
Canopy position	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.0012	< 0.0001
Summer period	< 0.0001	< 0.0001	0.1697	< 0.0001	0.0030	0.7220
Treatment	0.4215	0.7003	0.6914	0.1104	0.2902	0.2441
Species	0.0188	0.0019	0.0039	0.9769	0.0415	< 0.0001
Position × treatment	0.0003	–	–	–	–	–
Period × species	–	0.0291	< 0.0001	–	0.0197	–
Treatment × species	–	–	–	–	–	–
Position × period	–	–	0.0344	–	–	–
Period × treatment	–	–	0.0207	–	–	–
Position × treatment × species	–	–	–	–	0.0168	–

reached 44% (0.059 ± 0.008 and 0.033 ± 0.003 mol CO_2 (mol incident photon)$^{-1}$ for shade and sun foliage, respectively).

Grand fir had a greater Φ for each period than Douglas-fir (Figure 6B), although the two species were not always significantly different. In June, there was no difference in Φ between species (0.047 ± 0.005 and 0.044 ± 0.004 mol CO_2 (mol incident photon)$^{-1}$ for grand fir and Douglas-fir, respectively). However, by September, Φ differed by 49% between species (0.057 ± 0.007 and 0.029 ± 0.004 mol CO_2 (mol incident photon)$^{-1}$ for grand fir and Douglas-fir, respectively). Thus, Φ of grand fir rose as the season progressed, whereas Φ of Douglas-fir fell. The fertilizer treatments complicated predictions of Φ throughout the summer period (Figure 6C). Although the fertilizer treatments differentially affected Φ of grand fir and Douglas-fir over the summer (Table 2), we were unable to detect differences among treatment × period combinations.

Maximum assimilation rate also varied across the summer (Figure 7), increasing between June and July and then declining to a minimum in September. Mean $A_{\max}$ was greater for sun foliage than for shade foliage (4.58 ± 0.31 versus 3.02 ± 0.20 μmol m^{-2} s^{-1}).

Light compensation point (Γ) varied by species and canopy position (Table 2). Douglas-fir had a higher mean Γ than grand fir (22.15 ± 2.23 versus 10.22 ± 3.99 μmol m^{-2} s^{-1}) and Γ was higher in sun foliage than in shade foliage (21.66 ± 3.76 versus 11.98 ± 2.35 μmol m^{-2} s^{-1}).

We measured a three-way interaction for R_d between canopy position, species and fertilizer treatment. For both species, R_d (at 19 to 23 °C) decreased to its lowest rate in September, when $A_{\max}$ was also at its minimum. Mean R_d of Douglas-fir was highest in June and decreased thereafter (0.51 ± 0.07, 0.49 ± 0.07 and 0.24 ± 0.04 μmol m^{-2} s^{-1} for the three sampling periods, respectively). In contrast, mean R_d for grand fir peaked in July before falling to a minimum (0.31 ± 0.04,

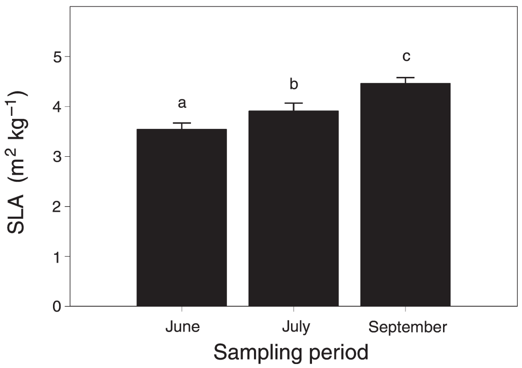

Figure 3. Relationship between mean specific leaf area (SLA) and sampling period for each study site. Bars represent means ± 1 SE. Different lowercase letters signify a significant pairwise comparison at $\alpha = 0.05$. Sample size (n) = 114, 114 and 113 for June, July and September, respectively.

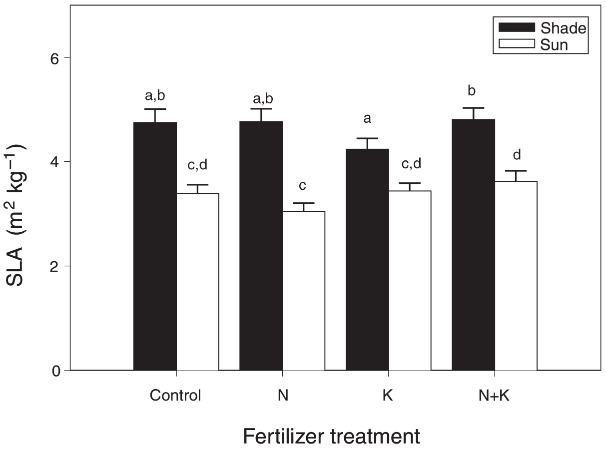

Figure 4. Relationship between mean specific leaf area (SLA) and fertilizer treatment and canopy position. Bars represent means ± 1 SE. Different lowercase letters signify a significant pairwise comparison at $\alpha = 0.05$. For shade foliage in the control, N and N + K treatments, $n = 41$ and the corresponding sample sizes for sun foliage are $n = 42$. For foliage in the K treatment, $n = 45$ for shade foliage and $n = 44$ for sun foliage.

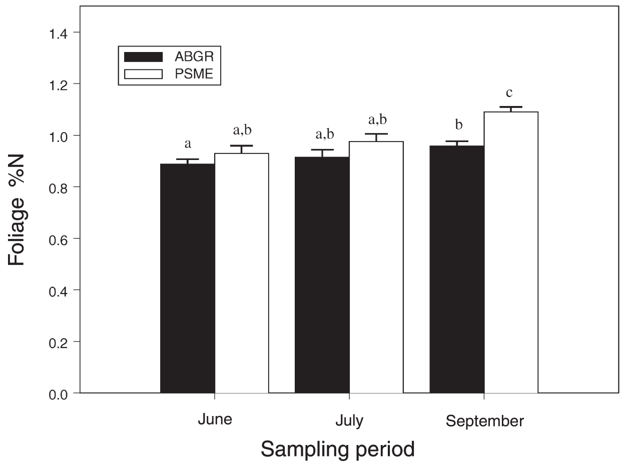

Figure 5. Relationship between percent nitrogen in the leaf calculated on a mass-to-mass basis (%N) and summer sampling period and species measured. Bars represent means ± 1 SE. Different lowercase letters signify a significant pairwise comparison at $\alpha = 0.05$. For grand fir (ABGR), n = 48, 50 and 44 for June, July and September, respectively. For Douglas-fir (PSME), n = 60, 59 and 58 for the same periods, respectively.

0.55 ± 0.09 and 0.29 ± 0.05 μmol m^{-2} s^{-1} for the three sampling periods, respectively).

There was a linear relationship between SLA and %N. The slope of an ordinary least squares regression line estimated the N concentration per area. The estimates were similar for shade and sun leaves (0.66 ± 0.08 and 0.67 ± 0.13 g N m^{-2}, respectively).

The relationship between %N and A_{max} changed with canopy position and sampling period (Figure 8). In shade foliage, the relationship was significant in September ($P = 0.05$), but not in June ($P = 0.09$) or July ($P = 0.88$). In sun foliage, the relationship was significant in June ($P = 0.04$), but not in July ($P = 0.40$) or September ($P = 0.36$). In sun foliage, higher %N was associated with lower A_{max}.

Over the whole study, differences in CO_2 assimilation rate at increasing PAR were evident between species and canopy positions (Figure 9). For both canopy positions, grand fir reached A_{max} at a lower irradiance than Douglas-fir. Shade leaves reached A_{max} and saturated at lower irradiances (200 and 400 μmol m^{-2} s^{-1} for grand fir and Douglas-fir, respectively) than sun leaves (600–700 μmol m^{-2} s^{-1} for both species). The assimilation rate for sun foliage continued to increase marginally up to irradiances of 1500 μmol m^{-2} s^{-1}.

Discussion

Forest process models are typically parameterized by a single value intended to characterize the entire canopy. We found spatial, temporal and interspecific variability in several key parameters. We discuss the observed patterns of variation in these model parameters and compare them to previously published results, attending to variation in methods used to estimate model parameters from leaf measurements. Our focus is

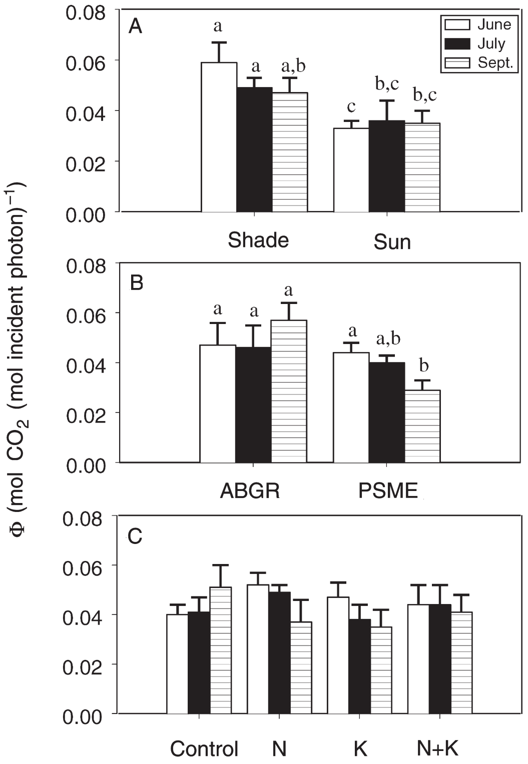

Figure 6. Relationship between mean apparent quantum yield (Φ) and summer sampling period for canopy position (A), species (B) and fertilizer treatments (C). Bars represent means ± 1 SE. Different lowercase letters between treatment means signify a significant pairwise comparison at $\alpha = 0.05$. In (C), no significant differences were detected between treatment and summer period combinations. In (A), n = 53, 55 and 48 for the June, July and September periods, respectively, for shade foliage, and n = 54, 53 and 50 for the same periods for sun foliage. In (B), n = 47, 49 and 41 for the sampling periods for *Abies grandis* (grand fir) (ABGR), and n = 60, 59 and 56 for the sampling periods for *Pseudotsuga menziesii* var. *glauca* (Douglas-fir) (PSME). In (C), sample size in the control, N and N + K treatments was n = 27 for each summer period, and for the K treatment, n = 30 for each summer period.

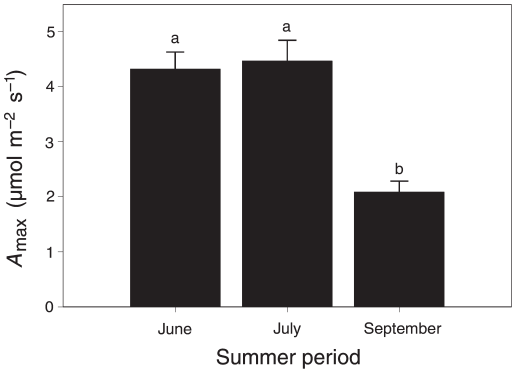

Figure 7. Relationship between maximum CO_2 assimilation rate (A_{max}) and summer sampling period. Bars represent means ± 1 SE. Different lowercase letters between treatment means signify a significant pairwise comparison at $\alpha = 0.05$. For June, July and September, n = 108, 109 and 102, respectively.

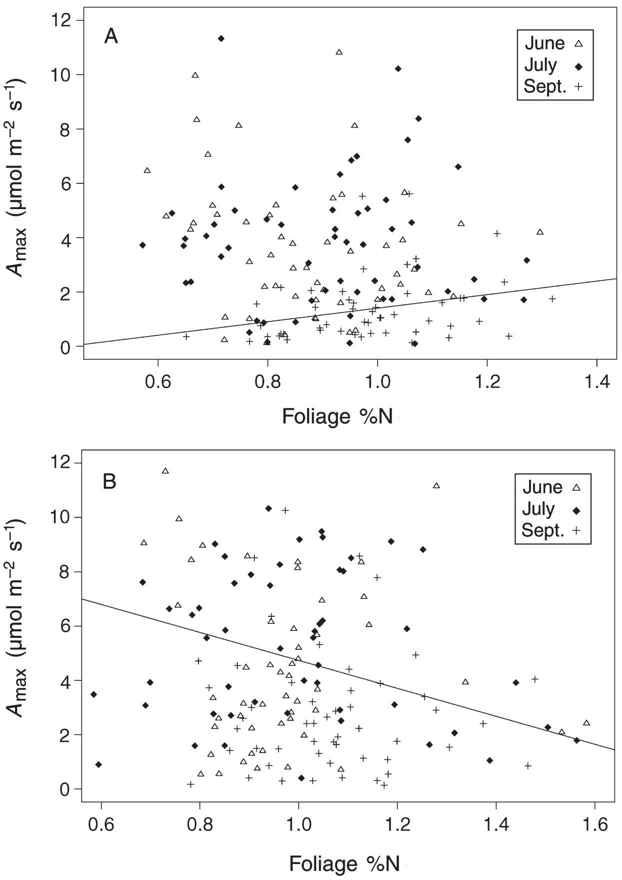

Figure 8. Relationship between percent nitrogen in the leaf calculated on a mass-to-mass basis (%N) and maximum CO_2 assimilation rate (A_{max}) for the shade and sun canopy positions (A and B, respectively). Confidence intervals for the shade data were $P = 0.09$, 0.88 and 0.05 for the June, July and September periods, respectively. Confidence intervals for the sun data were $P = 0.04$, 0.40 and 0.36 for the June, July and September periods, respectively. Regression lines were fit for significant relationships ($\alpha \leq 0.05$); specifically, the September period for the shade data and the June period for sun data. The September period of the shade data had an $r^2 = 0.08$ and a slope (± SE) of 2.5 ± 1.2, whereas the June period of the sun data had an $r^2 = 0.08$ and a slope (± SE) of –5.14 ± 2.47.

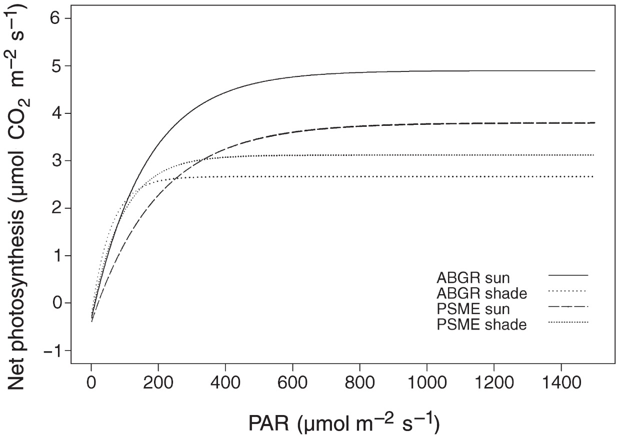

Figure 9. Photosynthetic light-response curves for both species and canopy positions generated by measuring assimilation rates at increasing irradiance. Each curve depicts the best fit of all measured photosynthetic rates (a total of 341 light curves) fit to a non-rectangular hyperbola. Abbreviations: ABGR = *Abies grandis* (grand fir); and PSME = *Pseudotsuga menziesii* var. *glauca* (Douglas-fir).

on quantum yield and foliar N concentration, and the potential application of these results in the parameterization and evaluation of process models.

Quantum yield (Φ)

The environmental parameters influencing Φ vary among studies, depending in part on how Φ is expressed. We note that our values are apparent quantum yields; that is, we expressed them relative to incident PAR, not absorbed PAR. With some important exceptions, leaf absorptance tends to be conservative among C_3 plants (Bjorkman and Demmig 1987). Quantum yields are also expressed in terms of either CO_2 consumption per incident photon, which is what we measured, or O_2 production per photon, which we denote Φ_{CO_2} and Φ_{O_2}, respectively, in the following discussion. We also note that our measurements were made at ambient oxygen concentration. Because Φ_{O_2} is often measured at sub-ambient O_2 to minimize photorespiratory consumption of oxygen, Φ_{O_2} is often much less sensitive to intercellular CO_2 concentration and temperature, two important controls over photorespiration (Singsaas et al. 2001). Most authors have found that Φ_{CO_2} is strongly dependent on intercellular CO_2 concentration and temperature (Ehleringer and Björkman 1977, Kirschbaum and Farquhar 1987, Leverenz and Öquist 1987). Most studies have found that Φ remains constant across light environments (Leverenz 1988, Bond et al. 1999, Schoettle and Smith 1999, Hättenschwiler 2001, Stenberg et al. 2001). However, Kubiske and Pregitzer (1996) and Grassi and Minotta (2000) found that Φ differed between sun and shade foliage of 1-year-old shoots. Others have reported a wide range of Φ values among species within the same forest ecosystem (Hättenschwiler 2001, Whitehead and Gower 2001). We found that Φ was significantly influenced by interactions between summer period and species, treatment and canopy position.

The broad range of values for Φ_{CO_2} reported in the literature may be partly related to three approaches employed in its estimation. First, there are different approaches for dealing with the Kok effect, which is the steepening of the light-response curve as net photosynthesis becomes negative at low PAR (Kirschbaum and Farquhar 1987, Singsaas et al. 2001). We made several measurements in the light-limited portion of the curve (PAR < 100 μmol m^{-2} s^{-1}) to ensure that we had a good estimate of the slope in this region. We fitted the data by nonlinear regression to a model that accounted for the convexity of the curve while the initial slope was being fitted. This allowed us to avoid the subjective issue of how many points to include in our estimate of the initial slope (Singsaas et al. 2001) because we fitted the whole model simultaneously. Second, we measured foliage from mature forests in the field, which remains relatively rare in forest ecology literature (Bassow and Bazzaz 1998). Third, many previous studies sampled small numbers of trees over narrow geographic ranges (Korol et al. 1991, Bassow and Bazzaz 1998, Bond et al. 1999). We used standard tree-climbing techniques to access 57 trees in eight stands distributed across a large region (Figure 1). Our ability to detect multiple sources of variation in Φ might be associated with our measurement and analysis techniques, the rarity of Φ measurements on mature trees and the statistical power gained by our relatively large sample size.

After correcting for leaf absorptance based on the mean value reported for conifers by Björkman and Demmig (1987), our estimates of Φ averaged 0.038 to 0.081 mol CO_2 (mol absorbed photon)$^{-1}$. The mean of these Φ values is similar to that reported for all C_3 plants (0.052 mol CO_2 (mol absorbed photon)$^{-1}$, Ehleringer and Björkman 1977), but it is below the mean Φ over all C_3 plants at the measurement temperature (~0.06 mol CO_2 (mol absorbed photon)$^{-1}$ at 19–23 °C, Leverenz and Öquist 1987). Our mean Φ value is similar to values reported for Scots pine during the growing season (0.052 to 0.055 mol CO_2 (mol absorbed photon)$^{-1}$, Leverenz and Öquist 1987), but above those recently reported for larch and black spruce (0.015 mol CO_2 (mol absorbed photon)$^{-1}$, Whitehead and Gower 2001) and the canopy Φ of 0.03 mol CO_2 (mol absorbed photon)$^{-1}$ assumed in the original description of the 3-PG model (Landsberg and Waring 1997).

Relationship between SLA and %N

The tendency for shade leaves to have a greater SLA than sun leaves is consistent with earlier observations (Niinemets 1997, Bond et al. 1999, Monserud and Marshall 1999, Evans and Poorter 2001). Leaf thinning is generally interpreted as a reallocation of carbon to increase light interception (Ellsworth and Reich 1993, Chen et al. 1996, Stenberg et al. 1999, Evans and Poorter 2001). The tendency for sun leaves to have higher N concentrations than shade leaves has also been reported (Mooney and Gulmon 1979, DeJong and Doyle 1985, Evans 1989, Reich et al. 1991, Evans and Poorter 2001). The redeployment of N to sun leaves has been interpreted as a reallocation of N to increase photosynthesis (Hollinger 1996, Bond et al. 1999). As a consequence of such reallocation, SLA and %N are often correlated across the canopy light gradient (Field 1983, DeJong and Doyle 1985, Oren et al. 1986, Hirose and Werger 1987, Givnish 1988, Ellsworth and Reich 1993, Niinemets 1997, Bond et al. 1999, Schoettle and Smith 1999, Grassi and Minotta 2000, Stenberg et al. 2001).

Specific leaf area and foliar %N also varied between Douglas-fir and grand fir. Grand fir is generally considered the more shade-tolerant of the two species. Previous studies have related the shade tolerance of plants to differences in their N partitioning and the N-use efficiency of photosynthesis (Seemann et al. 1987, Bond et al. 1999). Generally, shade-tolerant species have the highest photosynthetic carboxylation efficiency among species (Boardman 1977, Teskey and Shrestha 1985, Givnish 1988). Additionally, relative shade tolerance is the best predictor of growth and CO_2 exchange (Hättenschwiler 2001) and foliar morphology (Boardman 1977). In this study, SLA was greater for grand fir than for Douglas-fir in each combination of canopy position and sampling period.

Temporal variation was detected in SLA and %N. The SLA of 1-year-old foliage in both canopy positions increased as the growing season progressed. Seasonal differences in %N or SLA have been reported previously (Oren et al. 1986, Reich et al. 1991, Pierce et al. 1994). Because younger leaves expanded as the older foliage thinned or lost mass, we speculate that starch was mobilized and exported from the older foliage resulting in increased SLA (Figure 3). Foliar %N also increased between June and September, which would occur if starch were being mobilized. Alternately, the increase in %N may have been caused by increased N uptake. Because we were unable to detect a canopy position by sampling date interaction, we conclude that large quantities of N were not being redistributed within the canopy, contrary to what has been observed by other authors (DeJong and Doyle 1985, Hirose and Werger 1987, Bond et al. 1999, Evans and Poorter 2001). This temporal variation in SLA and %N is potentially important because models are often parameterized with constant values of these parameters. The variation raises questions about when in the year these parameters should be measured and what effects the variation has on model predictions. With respect to measurement time, if an average growing season value for these parameters is required, it appears that measuring at mid-season would provide the most representative value.

Applicability of measured parameter variation

The several forms of the process model PnET (PnET, PnET-II, and PnET-Day) assume that A_{max} is dependent on foliar N concentration (Aber and Federer 1992, Aber et al. 1995, 1996). In a sensitivity analysis of PnET-Day, estimates of gross carbon exchange were most sensitive to changes in A_{max} (Aber et al. 1996). Bassow and Bazzaz (1997) found that the correlation between N concentration and A_{max} was quite robust for northern hardwood forests. In contrast, the relationship is weak in our study and apparently in conifers in general. We found that the relationship between A_{max} and %N was significant on only one date for each species, and regression lines describing the relationship were in opposite directions. The tendency for conifers to show a weak correlation between A_{max} and N concentration has been noted before (Reich et al. 1998, Bond et al. 1999, Kloeppel et al. 2000). We speculate that these patterns may limit the ability of PnET to predict biomass production of the stands studied here.

Quantum yield plays a key role in the photosynthesis equation in the 3-PG model (Landsberg and Waring 1997). The seasonal variation in Φ within species and among crown positions suggests that if models are to be parameterized with leaf measurements, the Φ measurement would ideally account for these sources of variation. Note that our measurements of Φ are technically at $A = 0$ and, therefore, where c_i equals c_a. In a leaf with a high photosynthetic rate, c_i is much lower than c_a, especially in evergreen conifers (Marshall and Zhang 1994). Models exist for correcting Φ to these low c_i values (Brooks and Farquhar 1985, Singsaas et al. 2001). Comparisons of model predictions based on these c_i-adjusted Φ values to stan-

Table 3. Means (± SE) per site for each significant main effect noted in Table 2. Site numbers correspond to site descriptions in Table 1. Position refers to leaf location within the canopy, period is the date measured and species refers to either *Abies grandis* (ABGR) or *Pseudotsuga menziesii* var. *glauca* (PSME). Units: SLA, $m^2 kg^{-1}$; %N, $(mg\ mg^{-1})100$; Φ, mol CO_2 (mol incident photon)$^{-1}$; and A_{max}, $\mu mol\ m^{-2} s^{-1}$.

Predictor variables	Response variables	Sites							
		1	2	3	4	5	6	7	8
Position									
Sun	SLA	3.12 ± 0.17	3.04 ± 0.15	3.82 ± 0.23	2.44 ± 0.15	2.30 ± 0.24	3.34 ± 0.20	4.34 ± 0.20	4.20 ± 0.20
	%N	1.01 ± 0.02	0.95 ± 0.02	1.06 ± 0.02	0.83 ± 0.03	0.87 ± 0.05	1.02 ± 0.09	1.05 ± 0.04	1.21 ± 0.04
	Φ	0.031 ± 4.0e^{-3}	0.032 ± 2.0e^{-3}	0.047 ± 6.0e^{-3}	0.049 ± 2.1e^{-2}	0.036 ± 1.1e^{-3}	0.016 ± 5.0e^{-3}	0.047 ± 5.0e^{-3}	0.041 ± 5.0e^{-3}
	A_{max}	5.6 ± 1.5	4.4 ± 0.6	5.4 ± 0.6	6.2 ± 1.1	4.7 ± 0.9	0.9 ± 0.2	4.9 ± 0.6	3.1 ± 0.3
Shade	SLA	4.25 ± 0.21	4.50 ± 0.37	5.06 ± 0.16	3.28 ± 0.22	3.03 ± 0.27	4.18 ± 0.26	6.09 ± 0.24	5.85 ± 0.25
	%N	0.91 ± 0.02	0.97 ±0.03	0.96 ± 0.03	0.73 ± 0.02	0.82 ± 0.04	0.89 ± 0.04	1.06 ± 0.03	0.94 ± 0.03
	Φ	0.080 ± 2.1e^{-2}	0.043 ± 4.0e^{-3}	0.061 ± 8.0e^{-3}	0.051 ± 6.0e^{-3}	0.042 ± 6.0e^{-3}	0.033 ± 9.0e^{-3}	0.072 ± 6.0e^{-3}	0.051 ± 9.0e^{-3}
	A_{max}	4.3 ± 0.8	3.1 ± 0.4	3.5 ± 0.4	4.3 ± 0.7	3.3 ± 0.7	1.0 ± 0.4	2.8 ± 0.3	1.4 ± 0.1
Period									
May	SLA	3.11 ± 0.25	3.12 ± 0.21	4.00 ± 0.30	2.20 ± 0.17	2.52 ± 0.20	3.58 ± 0.34	4.71 ± 0.35	4.67 ± 0.25
	%N	0.93 ± 0.03	0.94 ± 0.02	0.96 ± 0.02	0.74 ± 0.02	0.72 ± 0.05	0.90 ± 0.03	1.01 ± 0.04	1.04 ± 0.06
	A_{max}	2.9 ± 0.8	3.1 ± 0.4	4.9 ± 0.5	8.1 ± 0.9	6.7 ± 0.9	1.0 ± 0.3	4.3 ± 0.7	2.7 ± 0.4
June	SLA	3.72 ± 0.26	4.19 ± 0.58	4.42 ± 0.25	2.63 ± 0.17	2.37 ± 0.27	3.86 ± 0.39	5.37 ± 0.32	4.99 ± 0.46
	%N	0.92 ± 0.03	0.95 ± 0.03	1.00 ± 0.04	0.71 ± 0.02	0.83 ± 0.03	0.91 ± 0.08	1.08 ± 0.05	1.10 ± 0.06
	A_{max}	8.7 ± 1.5	5.3 ± 0.6	6.1 ± 0.6	5.3 ± 1.5	4.0 ± 0.7	1.4 ± 0.6	3.8 ± 0.6	2.1 ± 0.4
September	SLA	4.23 ± 0.24	3.99 ± 0.20	4.98 ± 0.25	3.75 ± 0.24	3.11 ± 0.44	3.84 ± 0.25	5.57 ± 0.35	5.42 ± 0.27
	%N	1.02 ± 0.03	1.01 ± 0.03	1.08 ± 0.02	0.90 ± 0.03	0.98 ± 0.05	1.07 ± 0.11	1.09 ± 0.04	1.01 ± 0.05
	A_{max}	1.6 ± 0.4	2.9 ± 0.7	2.4 ± 0.5	1.8 ± 0.4	0.9 ± 0.3	0.5 ± 0.1	3.5 ± 0.6	1.8 ± 0.3
Species									
ABGR	SLA	3.98 ± 0.23	4.28 ± 0.38	4.93 ± 0.19	2.69 ± 0.19	3.58 ± 0.30	–	5.05 ± 0.26	5.21 ± 0.27
	%N	0.93 ± 0.03	0.98 ± 0.02	0.97 ± 0.03	0.74 ± 0.02	0.73 ± 0.04	–	0.99 ± 0.03	0.97 ± 0.03
	Φ	0.075 ± 2.1e^{-2}	0.040 ± 4.0e^{-3}	0.058 ± 7.0e^{-3}	0.066 ± 2.0e^{-2}	0.047 ± 1.1e^{-2}	–	0.065 ± 5.0e^{-3}	0.048 ± 8.0e^{-3}
PSME	SLA	3.41 ± 0.20	3.25 ± 0.19	4.00 ± 0.23	3.03 ± 0.22	2.44 ± 0.20	3.76 ± 0.18	5.38 ± 0.30	4.84 ± 0.29
	%N	0.98 ± 0.02	0.95 ± 0.03	1.04 ± 0.02	0.83 ± 0.03	0.87 ± 0.04	0.96 ± 0.05	1.13 ± 0.04	1.18 ± 0.05
	Φ	0.036 ± 5.0e^{-3}	0.034 ± 3.0e^{-3}	0.050 ± 7.0e^{-3}	0.030 ± 5.0e^{-3}	0.037 ± 7.0e^{-3}	0.024 ± 5.0e^{-3}	0.055 ± 7.0e^{-3}	0.045 ± 6.0e^{-3}

dard estimates may yield interesting results concerning model sensitivity. Stable isotope ratios could provide a convenient, integrated estimate of the c_i.

Mean parameter values based on significant ANOVA tests (Table 2) are presented in Table 3. These values describe the range of measured variation within the interior northwest region of the USA and may be useful for parameterizing and testing forest process models.

Conclusion

Key parameters of process models varied between species, temporally, and spatially within a regional fertilizer trial, indicating that parameterization of process models may require additional sampling to account for this variation, especially variation with canopy position and over the growing season. Based on the measured variation, the appropriateness of various bulking protocols can now be determined. As a rule of thumb, it appears that sampling during the middle of the growing season is most likely to capture the mean values of the parameters. We conclude that variation in model parameters must be considered as a potential source of error in ecosystem model predictions.

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