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Estimating leaf-level parameters for ecosystem process models: a study in mixed conifer canopies on complex terrain

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Summary Ecosystem process models are often used to predict carbon flux on a landscape or on a global scale. Such models must be aggregate and canopies are often treated as a uniform unit of foliage. Parameters that are known to vary within the canopy, e.g., nitrogen content and leaf mass per area, are often estimated by a mean value for the canopy. Estimating appropriate means is complicated, especially in mixed-species stands and in complex terrain.

We analyzed sources of variation in specific parameters with the goal of testing various simplifying assumptions. The measurements came from mixed-species forests in the northern Rocky Mountains. We found that, for three important parameters (nitrogen concentration and content, and leaf mass per area), a sample taken near the vertical center of the crown provided a good estimate of the mean values for the crown. Altitude (700–1700 m), solar insolation (4200–5400 MJ m^{-2} year^{-1}) and leaf area index (1–11) had negligible effects on the parameters; only species differences were consistently detected. The correlation between mass-based photosynthetic rates and mass-based nitrogen concentrations was much weaker than the correlation between area-based photosynthetic rates and area-based nitrogen concentration. Comparison of photosynthesis–nitrogen relationships for a wide variety of conifer species and sites revealed a broad general trend that can be used in models.

These results suggest important potential simplifications in model parameterization, most notably that canopy means can be estimated with ease, that complex terrain is a minor source of variation in these parameters and that use of one photosynthesis–nitrogen relationship for conifer species does not result in large errors. Species-to-species variation, however, was large and needs to be accounted for when parameterizing process models.

Keywords: inter-species variation, leaf nitrogen concentration, light-saturated photosynthesis, model parameterization, photosynthetic capacity, specific leaf area.

Introduction

Estimating gross primary production (GPP) is crucial to estimating carbon balance on ecosystem, regional and global scales. Process-based models (PBMs) are often employed to estimate GPP because measurement across large scales is difficult and time-consuming. Such models vary in the detail with which they represent processes (Robinson and Ek 2000, Mäkelä 2003, Medlyn et al. 2003). More detailed models scale leaf-level parameters to the canopy, and possibly to the landscape or regional level (Jarvis 1993). Less refined models treat forest stands (Aber and Federer 1992, Landsberg and Waring 1997) or landscape pixels as uniform vegetation units (Plummer 2000). One reason for the increased use of aggregate models is that less information is required to determine parameter values.

Three important leaf-level parameters that are necessary for the calibration of, or as inputs to, PBMs are: nitrogen (N) per unit leaf mass ($N\%$), leaf mass per area (LMA, the reciprocal of specific leaf area), and the derived parameter N per unit leaf area (N_{area}). Because plant canopies are commonly nitrogen-limited (Vitousek and Howarth 1991), $N\%$ integrates factors determining site N availability, and has been shown to correlate with mass-based photosynthetic rates (Field and Mooney 1986).

Leaf mass per area determines many leaf-level processes such as N- (Reich et al. 1998*a*) and water-use efficiency (Cordell et al. 1999, Lamont et al. 2002), and integrates leaf morphology and composition (Roderick et al. 1999). The product of $N\%$ and LMA, N_{area}, is correlated with area-based, light-saturated photosynthetic rates (Field and Mooney 1986) and has been used to derive estimates of canopy light-use efficiency (Medlyn 1996, Sands 1996, Rosati and DeJong 2003).

In mixed-species conifer forests on complex terrain, much variation exists in each of these parameters, on several scales. Known sources of variation include species (Rundel and Yoder 1998, Bond et al. 1999, Nippert and Marshall 2003), within-canopy variation due to shading (Niinemets and Valladares 2004), tree height (Marshall and Monserud 2003), leaf age (Hom and Oechel 1983), site fertility effects on $N\%$ and N_{area} (Brix 1981, Garrison et al. 2000, Pensa and Sellin 2003), leaf area index (Pierce et al. 1994) and altitude (Hultine and Marshall 2000). Spatial heterogeneity within the canopy makes it difficult to estimate mean parameter values for a given canopy pixel. Our first goal was to find a simple method for estimating canopy mean parameters and to eliminate the need to account for as many of these sources of variation as possible. We confined our study to current-year and 1-year-old foliage, but note that leaf age may be important in some conifer canopies (e.g., Bernier et al. 2001).

Our second goal was to test the relative contribution of the various sources of variation in $N\%$, LMA and N_{area} for mixed-species conifer forests on complex terrain, to identify the most important factors that must be considered when sampling across the landscape, and to rank these various sources of variation in order of importance.

Variations in light-saturated assimilation rate ($A_{\max}$) among conifer species and within the canopy, have been the subject of debate (Teskey et al. 1995). It has now become standard in many models to estimate $A_{\max}$ from N concentration (either area or mass-based) (Aber et al. 1996, Bernier et al. 2001). It is well known that the leaf-level $A_{\max}$ correlates with leaf N content (Natr 1972, Field and Mooney 1986, Reich et al. 1997), reflecting that a large proportion of leaf N is allocated to photosynthesis machinery (Evans 1989). However, it has been argued that the photosynthesis–nitrogen relationship either cannot be applied to conifer forests (e.g., Teskey et al. 1995) or that it is much weaker in conifers than in angiosperms (Aber et al. 1996). Our third goal was to test the hypothesis that N content or concentration explains the variation in $A_{\max}$ within canopies and between conifer species.

Materials and methods

We used three data sets in this study. Two sets were from previous studies (Marshall and Monserud 2003, Nippert and Marshall 2003), the third set was based on our own sampling of 22 plots in a mixed-species conifer forest in North Idaho. Both this study and Marshall and Monserud (2003) relied on data at the Priest River Experimental Forest (PREF). We will denote this study as PREF2001 (sampling occurred in 2001 and 2002), and Marshall and Monserud (2003) as PREF94 (sampling occurred in 1994). Nippert and Marshall (2003) sampled permanent plots from the Intermountain Forest Tree Nutrition Cooperative (IFTNC, Moscow, ID, USA) across the inland northwest USA; their data set is here denoted as INW. One-year-old foliage was sampled for the PREF2001 and INW data sets, whereas current-year foliage was sampled for the PREF94 data set. The canopy sampling strategy varied among the studies, and is described in detail below.

PREF2001

Study area The Priest River Experimental Forest (PREF) is located in the panhandle of northern Idaho, USA (48°21′ N, 116°45′–116°50′ W). The climate is transitional between a north Pacific coast and a continental type (Finklin 1983). Summers are generally characterized by cloudless skies and high midday vapor pressure deficits (VPD), often reaching 4–5 kPa. Mean annual precipitation is about 820 mm at 800 m a.s.l. and 1270 mm at 1700 m a.s.l. (Finklin 1983), showing a typical increase over altitude. A large proportion of the annual precipitation is snow, especially at higher altitudes. Twelve conifer species occur naturally in the PREF, with species composition largely determined by aspect and altitude (Cooper et al. 1991). Low-altitude sites in the PREF have dense mixed-species stands comprising (in order of importance) western red cedar (*Thuja plicata* Donn ex D. Don), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), the interior variety of Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), western white pine (*Pinus monticola* Dougl. ex D. Don), western larch (*Larix occidentalis* Nutt.) and ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.). Higher altitude stands comprise subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), lodgepole pine (*Pinus contorta* Dougl. ex Loud.), to a lesser extent Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and traces of whitebark pine (*Pinus albicaulus* Engelm.) and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.).

Sampling design The goal of the experimental design was to include a wide variety of environmental conditions. To achieve this, the study area was stratified by altitude and solar insolation and 36 plots were randomly allocated in these strata. The plots were 90 × 90 m, thus matching satellite imagery pixels (Landsat; see Pocewicz et al. 2004). This strategy resulted in a wide range of canopy conditions, especially species composition, structure, age and management history. More details are provided by Duursma et al. (2003) and Pocewicz et al. (2004). For this study, we sampled 22 of the 36 randomly located plots in the summers of 2001 and 2002. We chose plots achieving the widest variation in altitude and solar insolation classes, but avoiding plots that were far from roads. Estimates of leaf area index (LAI) and forest inventory variables were available at five sampling locations within each plot (Duursma et al. 2003). Trees at these five points, or a subset of these points, were sampled for foliage. At each sampling point, one tree was sampled with the aid of climbing equipment. The closest dominant or codominant tree to the sampling point was chosen, but diseased or leaning trees were excluded. When possible, one or two nearby trees were sampled from the climbed tree with the use of a 4-m pruning pole. During the first season, few western larch and lodgepole pine trees were sampled, but during the second season, branches of these species were taken in four plots using a rifle. The goal was to sample six shoots from each tree, including both the climbed tree and adjacent trees. Two shoots were sampled from upper, middle and bottom thirds of the canopy. The heights of the sampled shoots were measured with a tape. Within each crown third, two samples were taken from the same height, but from main branches as far apart as possible. Samples were placed in plastic bags in a small cooler on ice until the end of the day when they were stored at –20 °C.

Leaf mass per area Leaf mass per area was determined on the previous season's foliage, with the exception of cedar and larch. For the purpose of calculating LMA in western red cedar, which has no distinct annual shoots, the last 10 cm of the shoot, including the apex with all its foliage, was treated as a single leaf. Leaf mass per area of Western larch was determined on one current-year short shoot, which typically carried 20–30 needles. The foliage was placed flat on a digital scanner, together with a dark metal rod of known area. Projected area was estimated from the images with SigmaScan Pro (Aspire Software, Leesburg, VA). Foliage was then placed in paper bags and dried at 70 °C for 72 h and weighed. We calculated LMA on a projected-area basis.

Gas exchange Instantaneous light-saturated net photosynthetic rates (A_{max}) were measured with an LI-6400 (Li-Cor, Lincoln, NE) in a 2 × 3 cm cuvette. For each tree, measurements were made on one foliated shoot from top, middle and bottom thirds of the canopy. The shoot was placed outside the cuvette, with as many needles inside the cuvette as possible without overlap. Needles were removed from the twig to prevent self-shading. We monitored A_{max} for 3 min at a photosynthetic photon flux (PPF) of 1300 µmol m^{-2} s^{-1} and a carbon dioxide concentration ($[CO_2]$) of 400 ppm. Temperature and humidity were close to ambient and measurements were made within 20 min of shoot excision.

PREF94

Monserud and Marshall (1999) and Marshall and Monserud (2003) sampled three species (Douglas-fir, western white pine and ponderosa pine) in eight mixed-species stands in the PREF. A total of 66 trees were harvested and eight branches were sampled vertically throughout the crown of each tree. Height of crown base was defined as the height of the live whorl above the highest two consecutive dead whorls and was measured after felling. The number of branches in each whorl from which the sample branch was taken was recorded. From near the end of each branch, 10–25 current-year needles were collected. Leaf mass per area data for these samples are available (Marshall and Monserud 2003) and we analyzed the same samples for *N%*.

INW

Nippert and Marshall (2003) sampled a total of 64 Douglas-fir trees and 50 grand fir trees, three times between June and September 2001, on eight sites throughout the inland northwest USA. At each site, there is an installation of the Intermountain Forest Tree Nutrition Cooperative (IFTNC), consisting of four fertilizer treatment plots. At the time of sampling, fertilization had not been applied for at least 5 years. Foliage expanded in the previous season was collected near the canopy top and from the lowest living branch. Each sample was analyzed for LMA, *N%*, and instantaneous gas exchange rates.

Nitrogen concentration and content

Tissue N analyses were performed at the University of Idaho Stable Isotope Laboratory. Foliar samples were oven-dried at 70 °C for at least 72 h and ground to a fine powder in a ball mill. Nitrogen concentration (*N%*; g N per 100 g dry mass) was determined with a CN-2400 EA (Thermo Electron, Milan, Italy) coupled to a Finnigan-MAT delta + (Finnigan- MAT, Bremen, Germany). Leaf N per unit leaf area (N_{area}; g m^{-2}) is the product of LMA and *N%*/100.

Data analysis

Sampling for the canopy mean We used the PREF94 data set to compare three estimates of the canopy mean for LMA, *N%* or N_{area}. The first estimate, the foliage mass-weighted estimate, is the most comprehensive. Assuming the branches within a whorl are relatively homogeneous, the foliage mass for whorl i ($W_{fol}(i)$) is obtained by multiplying sample branch foliage mass by the number of branches in the whorl. The foliage mass-weighted canopy mean for some variable is estimated with Equation 1:

$$\bar{Y}_1 = \frac{\sum_{i=1}^{n} W_{fol}(i) Y_i}{\sum_{i=1}^{n} W_{fol}(i)} \tag{1}$$

Equation 1 provides a weighted mean of Y by foliage mass. A second estimate is simply the mean of all samples (Equation 2),

$$\bar{Y}_2 = \frac{1}{n} \sum_{i}^{n} Y_i \tag{2}$$

A third estimate is simply to take the sample closest to the mid-canopy ($\bar{Y}_3$), which was selected from among the eight samples from the tree.

We used the PREF94 data set to obtain these three estimates, which were compared as follows. First, we carried out linear regressions of $\bar{Y}_2$ and $\bar{Y}_3$ against $\bar{Y}_1$ (the most comprehensive estimate). Root mean squared error (RMSE), which can be interpreted as the residuals standard deviation, and r^2 were used as indicators of goodness of fit. A test of the significance of the intercept and deviation of the slope from unity was performed. The null hypothesis of no difference is rejected less freely by this test at smaller sample sizes, however, failure to reject the null hypothesis is no evidence in favor of it (Parkhurst 2001). We also performed equivalence tests (Wellek 2003, Robinson and Froese 2004) and considered the two estimators as equivalent when they gave estimates that were within 10% of each other. To test this, we computed the statistic S, defined as:

$$S = \frac{Y_i - \bar{Y}_1}{\bar{Y}_1} \tag{3}$$

where Y_i is $\bar{Y}_2$ or $\bar{Y}_3$. We tested the null hypothesis that $|S| > 0.1$ (the estimates are different) at the $\alpha = 0.05$ level (see Robinson and Froese 2004), against the alternative hypothesis that the estimates are similar (i.e., within 10% of each other).

Complex terrain The effects of altitude and solar insolation on LMA, N_{area} and $N\%$ were tested with the PREF2001 data set. The data come from a nested design: samples within crown thirds, crown thirds within trees, trees within sampling points and sampling points within plots. Mixed-effects models can account for multiple nesting of data (Pinheiro and Bates 2000) with the use of nested random effects. The fixed effects tested were species, altitude, solar insolation and LAI. Estimates of solar insolation (solar radiation integrated over a year) were obtained with MT-CLIM (mountain climate simulator, Version 4.3, University of Montana, Missoula, MT), with a correction for the surrounding terrain (Duursma 2004) and estimates of LAI were from Duursma et al. (2003). Solar insolation estimates varied from 4200 to 5400 MJ m^{-2} $year^{-1}$ and LAI from about 1 to 11 m^2 projected leaf area m^{-2} ground. Crown third is treated as a random effect, but see Duursma (2004) for modeling of N_{area}, LMA and $N\%$ as a function of depth in the canopy.

Five mixed-effects models were constructed; each had different fixed effects but the same nested random effects. The tested sets of fixed effects were: (1) none; (2) species; (3) species and altitude; (4) species and solar insolation; and (5) species and LAI. Altitude, solar insolation and LAI were tested together with species, because these variables can better be interpreted as having a conditional effect on leaf-level variables after variation due to species has been accounted for. Apart from the usual significance testing, the five models were compared using Akaike's information criterion (AIC) and RMSE. In nested models, the RMSE can be computed as the standard deviation of the residuals at each of the levels of the random effects and at the population level (Pinheiro and Bates 2000). Because our objective was to investigate whether each of the fixed effects could explain variance across the landscape, we report RMSE of the population predictions only. Log transformations of each of the variables were necessary to meet model assumptions (cf. Pinheiro and Bates 2000).

The variance of each of the variables can be attributed to plot, sampling point, tree or crown third ("variance components") using the random effects. This procedure can pinpoint the more important sources of variation, and thus help in recommendations for future studies (e.g., Suomela and Ayres 1994). The fixed effects altitude, solar insolation and species were all included as fixed effects for the construction of a variance components model. This way, the variance between plots (and other levels) was corrected for species composition and possible complex terrain effects and the variance components must therefore be interpreted accordingly.

The photosynthesis–nitrogen relationship We tested the relationships between area-based $A_{\max}$ and N_{area} and mass-based $A_{\max}$ and $N\%$ with the gas exchange data sets of PREF2001 and INW. We analyzed these relationships by species by linear regression.

Results

Estimating the canopy mean

Three estimates of the canopy mean were obtained for each tree: (1) the foliage mass-weighted mean; (2) the simple mean; and (3) the sample closest to the mid-crown. The last two estimates were compared with the weighted mean (Table 1) by linear regression and equivalence testing. For the comparison between the weighted mean and the sample closest to the middle of the canopy, intercepts did not differ from zero and slopes did not differ from unity, indicating a lack of evidence that the measurement closest to mid-canopy was a significantly biased estimate of the canopy mean (Figures 1 and 2). This is not, however, evidence in favor of similarity of the two estimates (Parkhurst 2001). Based on equivalence testing, all null hypotheses of difference were rejected at $\alpha = 0.05$. This means that the mid-canopy samples were statistically similar (within 10%) to the foliage mass weighted canopy mean.

For comparison with the study of Pierce et al. (1994), the effect of LAI on canopy mean variables was tested when $N\%$, N_{area} and LMA were averaged across all species in a plot (Figure 3). No relationship between LAI and LMA or $N\%$ was found ($P > 0.10$), but there was a negative effect of LAI on N_{area} ($P = 0.037$, $R^2_{\mathrm{adj}} = 0.16$).

The photosynthesis–nitrogen relationship

Field measurements of $A_{\max}$ were weakly related to N, when expressed on a leaf area or a mass basis (Figure 4). When analyzed for each species separately, area-based comparisons were significant ($\alpha = 0.05$) for grand fir, western hemlock and western red cedar, but not significant for the other species. The mass-based comparison was significant only for western red cedar.

Table 1. Statistics of comparison between the weighted mean and the simple mean nitrogen concentration ($N\%$), nitrogen content (N_{area}) and leaf mass area (LMA), and comparison between the sample closest to the middle and the weighted mean. For each comparison, linear regression was performed, the intercept (β_0) tested against zero and the slope (β_1) against unity, and r^2 is reported. The mean absolute difference (MAD) between the estimates, and the residuals standard deviation (RMSE) are also given. For all six comparisons, the null hypothesis of dissimilarity was rejected (see text), indicating statistical similarity.

	Simple mean–weighted mean					Mid-canopy sample–weighted mean				
	r^2	P (H$_0$: $\beta_1 = 1$)	P (H$_0$: $\beta_0 = 0$)	RMSE	MAD	r^2	P (H$_0$: $\beta_1 = 1$)	P (H$_0$: $\beta_0 = 0$)	RMSE	MAD
LMA	0.97	0.89	0.53	9.4	7.1	0.90	0.67	0.43	19.7	13.9
$N\%$	0.81	0.011	0.0038	0.045	0.04	0.63	0.29	0.39	0.096	0.075
N_{area}	0.95	0.68	0.096	0.15	0.13	0.74	0.19	0.097	0.35	0.28

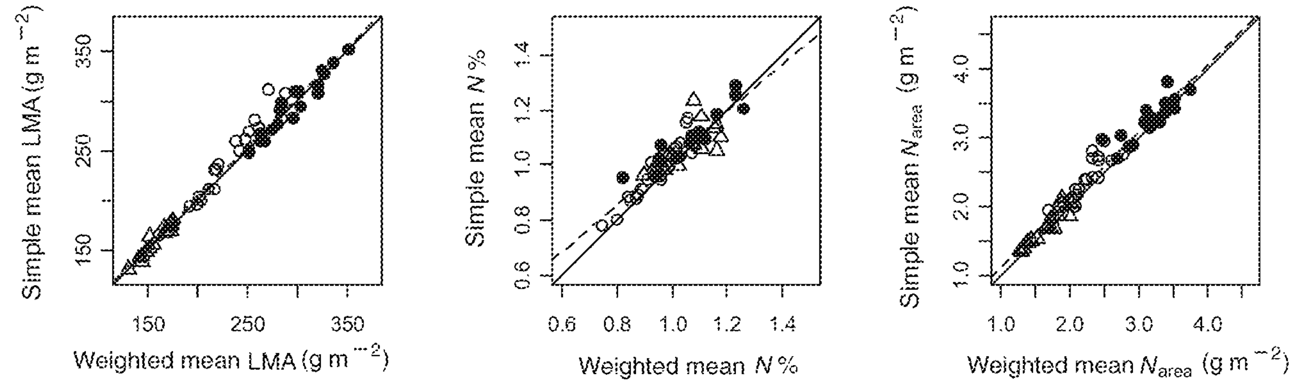

Figure 1. Comparison of weighted and simple mean canopy estimates. The weighted mean was obtained by weighting the variable by the foliage mass distribution. The simple mean is the mean of all samples in the crown. Each value represents one tree. Symbols: ○ = Douglas-fir; ● = ponderosa pine; and △ = western white pine. Dashed lines are regression lines. The solid lines are 1:1 lines. Abbreviations: LMA = leaf mass per area; *N*% = nitrogen concentration; and N_{area} = leaf nitrogen per unit leaf area.

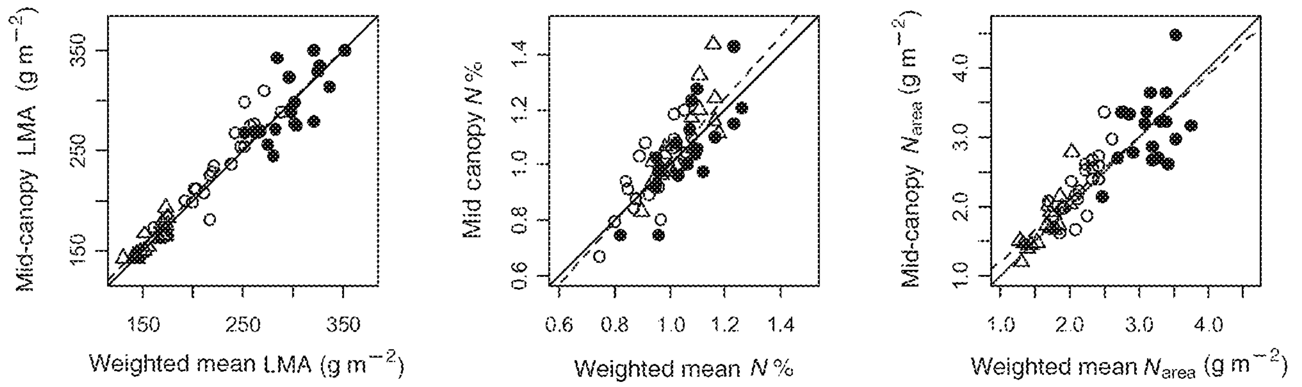

Figure 2. Comparison of weighted mean and mid-canopy estimates. The weighted mean was obtained by weighting the variable by the foliage mass distribution. The mid-canopy estimate was the value for the sample closest to the mid-canopy. Each value represents one tree. Symbols: ○ = Douglas-fir; ● = ponderosa pine; and △ = western white pine. Dotted lines are regression lines. The solid line is a 1:1 line. Abbreviations: LMA = leaf mass per area; *N*% = nitrogen concentration; and N_{area} = leaf nitrogen per unit leaf area.

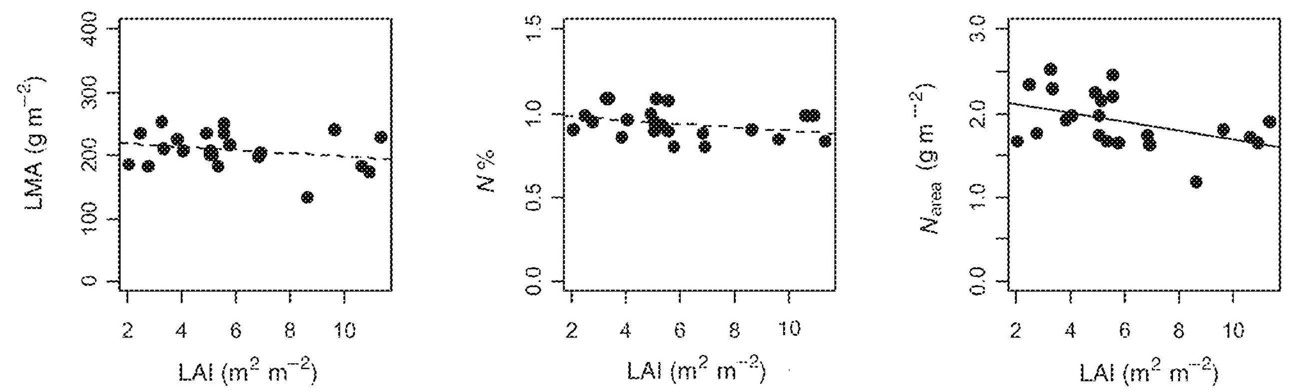

Figure 3. Relationships between canopy mean leaf mass area (LMA), nitrogen concentration (*N*%) and nitrogen content (N_{area}) and leaf area index (LAI) for the PREF2001 data set. Each value represents a plot. Error bars are not shown because they were small compared with the size of the symbols. Dashed lines denote a nonsignificant regression, and solid lines denote a significant regression ($P < 0.05$).

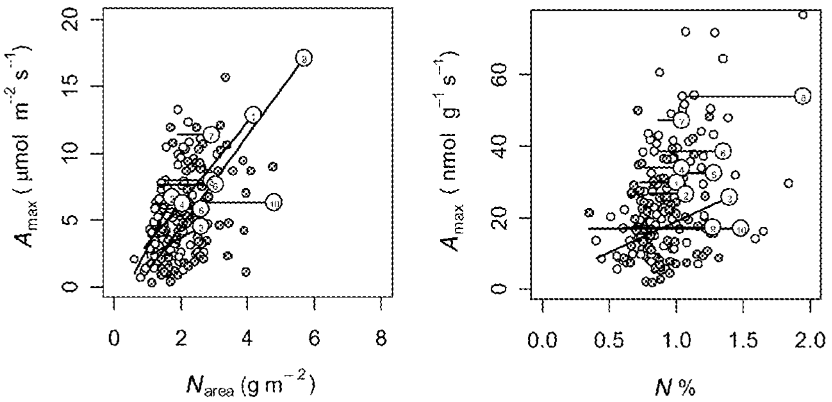

Figure 4. Area-based and mass-based comparisons between light-saturated net carbon dioxide (CO_2) assimilation (A_{max}) and leaf nitrogen (N% or N_{area}) for the PREF2001 (○) and INW (◍) data sets. Horizontal dashed lines denote a nonsignificant regression (α = 0.05). Numbered lines denote: 1, *Abies grandis* (PREF2001); 2, *Tsuga heterophylla*; 3, *Thuja plicata*; 4, *Pseudotsuga menziesii*; 5, *Larix occidentalis*; 6, *Abies lasiocarpa*; 7, *Pinus contorta*; 8, *Pinus monticola*; 9, *Abies grandis* (INW); and 10, *Pseudotsuga menziesii* (INW).

Table 2. The P values for independent variables: species, altitude, solar insolation and leaf area index (LAI) from the mixed model results. In each case, the P value is from an F test against zero with numerator degrees of freedom (df) 9, and denominator df 60, except for species (8 and 69 df).

Variable	Species	Altitude	Solar insolation	Leaf area index
LMA	< 0.0001	0.62	0.29	0.037
N_{area}	< 0.0001	0.25	0.76	0.71
N%	< 0.0001	0.069	0.49	0.27

Table 3. Mean of leaf mass area (LMA), nitrogen concentration (N%) and nitrogen content (N_{area}) for the nine species sampled in the Priest River Experimental Forest. Means and standard errors (in parentheses) were estimated with a mixed-effects model with species as the fixed effect, and accounting for plot, sampling point and tree clustering through random effects. The sample size (n) is the total number of samples, six samples were taken from every tree.

Species	LMA	N%	N_{area}	n
Abies grandis	218.0 (8.30)	0.92 (0.039)	1.99 (0.085)	72
Abies lasiocarpa	232.0 (8.2)	1.05 (0.038)	2.44 (0.083)	82
Larix occidentalis	136.4 (9.1)	1.53 (0.041)	2.10 (0.094)	49
Pinus contorta	256.6 (9.4)	0.96 (0.043)	2.55 (0.095)	60
Pinus monticola	199.6 (14.0)	1.03 (0.065)	2.03 (0.15)	24
Pinus ponderosa	291.5 (11.0)	1.05 (0.051)	2.99 (0.11)	36
Pseudotsuga menziesii	227.7 (5.9)	0.89 (0.028)	2.04 (0.058)	178
Thuja plicata	240.6 (4.9)	0.81 (0.024)	1.90 (0.049)	282
Tsuga heterophylla	147.3 (6.6)	0.97 (0.031)	1.41 (0.066)	134

Complex terrain

Significant species effects on LMA, N% and N_{area} were found (Table 2). Both LMA and N_{area} varied twofold among species (Table 3), but inter-species variation in N% was comparatively small, with one exception. Western larch showed a much higher N% than the evergreen species. Further, the RMSE of the fitted model decreased substantially when species was used as an explanatory variable (Table 4). Altitude and solar insolation had no significant effects on the three leaf-level parameters, and no reduction in RMSE was found when altitude or solar insolation was added to the model (Table 4). Significant effects of LAI were found on LMA (P = 0.037; Table 2), but the RMSE decreased only marginally when LAI was added to species as an explanatory variable (Table 4), indicating that the effect was weak. Analyzing the data for each species separately, we found that western larch N_{area} increased significantly with altitude (Figure 5), but N% did not. No other species showed such an increase; for this reason, altitude was not significant in the full model. The relationship between LAI and LMA was significant only for hemlock (P = 0.0132) and ponderosa pine (P = 0.04), and again LAI explained little of the variation (not shown).

The variation was partitioned into plot, sampling point, tree and crown position using the mixed model (see Table 5), after accounting for species and complex-terrain effects. The largest sources of variation for LMA and N% were crown position and plot. For N_{area}, the plot effect was small, but crown position accounted for 46% of the variation. The tree effect, within the

Table 4. Root mean squared error (RMSE) for mixed models fitting leaf mass area (LMA), nitrogen concentration (N%) or nitrogen content (N_{area}) to different fixed effects. The RMSE can be interpreted as the residuals standard deviation, and here is given as the RMSE at the population level. Units are in logarithms of each of the variables because this transformation was necessary to meet model assumptions (and the RMSE cannot be simply back-transformed). Note the large relative reduction in RMSE when the species effect is added, but virtually no reduction after adding other fixed effects. Abbreviation: LAI = leaf area index.

Fixed effect	RMSE		
	log(LMA)	log(N%)	log(N_{area})
None	0.289	0.229	0.312
Species	0.206	0.170	0.244
Species, altitude	0.204	0.169	0.243
Species, solar insolation	0.206	0.168	0.239
Species, LAI	0.201	0.169	0.242

sampling point, was a minor source of variation (0.1–3.2%), except for N% (18.3%).

Discussion

Estimating the canopy mean

Aggregated models require that canopy physiology parameters be expressed as the mean of the canopy over a stand or a pixel, where the stand or pixel is assumed to be a uniform unit. Because of the complexity of forest stands, which may include several species, uneven age distribution and a range of slopes and aspects, this seems like a formidable task. Some models even describe vertical variation in canopy traits, e.g., LMA (Aber et al. 1996, Bernier et al. 2001). However, our results show that sampling close to mid-canopy (halfway between top and bottom of the crown) results in estimates of the canopy mean that do not have detectable bias for N%, N_{area} and LMA in three conifer species. We suggest, therefore, that field sampling can be simplified by sampling only in the mid-crown.

In a transect study across a mostly conifer-dominated vegetation in Oregon, Pierce et al. (1994) investigated trends in LMA, N_{area} and N% across diverse sites. They identified several relationships at the regional scale: (1) LAI is negatively correlated with LMA; (2) LAI is positively correlated with canopy mean N%; and (3) LAI is negatively correlated with canopy mean N_{area}. This result was not surprising because an increased LAI is achieved by adding successive layers of shade leaves under the sun leaves. Shade leaves tend to have lower LMA and N_{area} as a result of acclimation to light (Niinemets 1997, Stenberg et al. 1998, Bond et al. 1999). However, we found no significant relationships between LAI and N% or LMA and only a weak effect of LAI on N_{area}. Our study differs from the transect study of Pierce et al. (1994) in several respects. The transect study sampled forests with some of the highest LAIs in the world (Gholz et al. 1976) and the transect continued inland over two mountain ranges and into the rain shadow on the other side (see Peterson and Waring 1994). Thus it covered a broader range of conditions, from wetter and more maritime, to drier and more continental, than any sites in our study and it also sampled a broader range of species. Although our sample included a rather large range in LAI, the absence of an effect of LAI on N% and LMA suggests that LAI effects on these parameters do not need to be accounted for when estimating canopy mean parameters for forests in the northern Rocky Mountains.

Complex terrain

We sampled nine conifer species across a complex altitudinal gradient spanning 1000 m. No significant effects of altitude or solar insolation were found on LMA, and altitude was significant only for N% and N_{area} of western larch (Figure 5). Larch was the only deciduous species in the sample, which may account for its unique pattern of variation (Gower and Richards 1990, Marshall and Zhang 1994, Kloeppel et al. 2000). Previous studies have found significant positive correlations of alti-

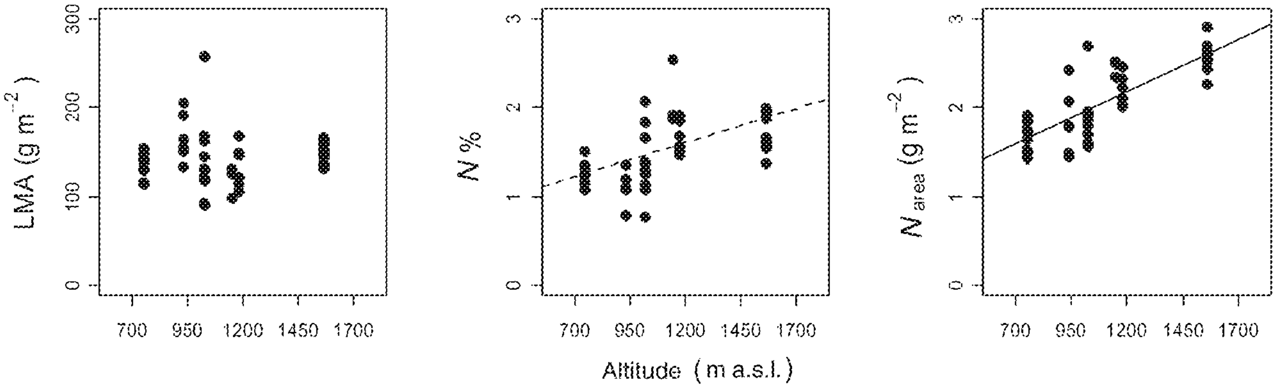

Figure 5. Effect of altitude on leaf mass area (LMA), nitrogen content (N_{area}) and nitrogen concentration (N%) for western larch, the only species in this study to show significant altitude effects. Parameters LMA (P = 0.8) and N% (P = 0.19) did not change with altitude, whereas N_{area} increased as: $N_{\text{area}} = 0.79(0.26) + 1.1(0.24)A$, $P = 0.0078$, where A is altitude (in km) and SE are in parentheses.

Table 5. Variance components of leaf mass area (LMA), nitrogen concentration ($N\%$) and nitrogen content (N_{area}) at four different scales for the PREF2001 data set. The standard deviation (σ) of the random effect is given both in the units of the variable, and as a percentage of the total σ. The residual can be interpreted as the σ of observations within a crown third. Note the low σ for the tree, and the high σ for the crown third components.

Source	LMA		$N\%$		N_{area}	
	(g m^{-2})	%	(g 100 g^{-1})	%	(g m^{-2})	%
Plot	18.0	21.24	0.082	22.26	0.027	3.33
Sampling point	12.0	13.92	0.053	14.47	0.130	15.97
Tree	0.10	0.12	0.067	18.32	0.026	3.18
Crown third	34.0	39.79	0.077	20.81	0.380	46.80
Residual	21.0	24.94	0.089	24.14	0.250	30.72

tude with LMA and $N\%$, and therefore also N_{area} (Körner and Diemer 1987, Körner 1989, Friend and Woodward 1990, Vitousek et al. 1990); however, these studies did not include conifer species. Hultine and Marshall (2000) found significant increases in LMA, $N\%$ and N_{area} for some, but not all, of the studied conifer species. Their study was conducted over an altitude gradient of 1800 m, whereas the PREF2001 data set was collected over a gradient of only 1000 m. These results reinforce the finding that transect studies tend to detect different sources of variation when the range of environmental conditions along the transect is increased.

On complex terrain, especially with steep slopes, marked variation exists in the amount of solar radiation received annually (solar insolation; e.g., Olseth and Skartveit 1997), in our study from 4200 to 5400 MJ m^{-2} $year^{-1}$ (Duursma 2004). Because light availability affects plant growth and development at most scales (Boardman 1977, Givnish 1988, Niinemets and Valladares 2004), it can be assumed that solar insolation affects canopy physiological parameters. We predicted that canopies on low solar insolation sites would have lower LMA than canopies on high insolation sites, similar to the influence of light availability within the canopy on LMA. However, we found no effect of solar insolation on LMA, likely because variation in light availability within canopies is many times greater than across complex terrain.

We found relatively large variations in LMA, N_{area} and $N\%$ among species (Table 3) when averaged over all samples. Western larch showed the lowest LMA, which is consistent with the findings of Kloeppel et al. (2000), although western hemlock also had a low LMA. Western larch had the highest $N\%$, which is also consistent with previous studies (Kloeppel et al. 2000), and that reinforces the evidence that thinner leaves (lower LMA) tend to have higher $N\%$ (Schulze et al. 1994, Roderick et al. 1999). The remaining eight evergreen conifer species showed relatively little variation in $N\%$ (0.8–1.05%). As a result of the variation in LMA and $N\%$, N_{area} varied twofold between western hemlock (1.4 g N m^{-2}) and ponderosa pine (3.0 g N m^{-2}), with the other seven species taking intermediate positions. The interspecies variation reported here is consistent with many previous reports for conifer species (Reich et al. 1995, Rundel and Yoder 1998, Kloeppel et al. 2000).

For LMA and N_{area} (but not $N\%$), surprisingly little of the variation was among trees on a sampling point. This similarity in LMA and N_{area} may be associated with the uniform light environment within a sampling point. In contrast, $N\%$ is determined less, if at all, by the light environment (Niinemets 1997), and differences in $N\%$ among adjacent trees may indicate patchy distribution of N availability belowground. A similar study of sources of variation in leaf traits in *Betula pubescens* J. F. Ehrh., including LMA and $N\%$, found that tree-to-tree variation was a large source of variation (Suomela and Ayres 1994). In our study, the second most important source of variation in LMA and $N\%$ was among plots, even after plot differences in altitude and solar insolation were accounted for. Variation in N_{area} among plots was low, perhaps resulting from a significant interaction between LMA and $N\%$ (Roderick et al. 1999), which may cancel out variation in N_{area}.

Implications for model parameterization

Our results suggest two important potential simplifications in the parameterization of canopy models for forests in the northern Rockies. First, if canopy means are sufficient to parameterize the selected models, samples of LMA, $N\%$ and N_{area} need be collected only in the mid-crown (e.g., Landsberg and Waring 1997). Second, there is little variation in these traits with topographic position, except in the one deciduous species measured, western larch. The variation among trees leads us to suggest that replication of the mid-crown sampling is required for accurate estimates of the canopy mean. The large inter-species variation points to the need to account for species composition in these conifer forests. We did not account for the effect of leaf age on $N\%$ and LMA, although its effect on the canopy mean may be significant (Hom and Oechel 1983, Oleksyn et al. 1997, Warren and Adams 2000). In a modeling study in *Abies balsamea* (L.) Mill., Bernier et al (2001) found 9% bias in canopy photosynthesis when ignoring age effects on A_{max}, and suggested that samples of A_{max} should be obtained on foliage of mean age in the canopy. More work is needed to quantify the gain in predictive power when the effects of leaf age on canopy parameters are taken into account.

The photosynthesis–nitrogen relationship

In our study, area-based estimates of net photosynthesis and N content were correlated in only three species: grand fir (both PREF2001 and INW data sets), western hemlock and western red cedar. The mass-based comparison was significant only for western red cedar (Figure 4). This mostly negative result is consistent with other studies that have found weak relationships between these traits for conifers (Reich et al. 1995, Teskey et al. 1994, 1995). Some studies even found no significant relationship between N_{area} or $N\%$ and A_{max} (e.g., Yoder 1992, Porté and Loustau 1998, Nagel and O'Hara 2001, Will et al. 2001).

There have been several reviews of the photosynthesis–nitrogen relationship (Field and Mooney 1986, Reich et al. 1997), but this relationship has not been analyzed across conifer species exclusively. Reich et al. (1995) included several conifer species, but analyzed the relationship only across means for a few conifer species. Similarly, Field and Mooney (1986) included only a few non-conifer evergreen species in their analysis. To place our results in a broader context, we reviewed the literature for reported relationships between N concentration and A_{max}, both area- and mass-based, among conifer species (see Appendix). When possible, nonsignificant relationships were also obtained from the literature to avoid biasing our review. Each of the reviewed studies showed variation in $N\%$ or N_{area} or both, with the variation originating from various sources. The results for this review and a list of the studies are shown in Figure 6. More details of the review are presented in Duursma (2004). Although slopes and intercepts of both area- and mass-based comparisons varied substantially among studies, when all were plotted together, a broad trend appeared (Figures 6 and 7). This trend was especially apparent for the area-based comparison. A few studies predicted exceptionally low area-based A_{max}, given N_{area} (Figure 6), but all were conducted with desert trees and shrubs (DeLucia and Schlesinger 1991, Miller et al. 1991*a*, 1991*b*, Marshall et al. 1994), which are likely to experience stomatal closure due to low water potentials and high VPD.

The narrow range of leaf N found in conifers (e.g., Reich et al. 1995) may explain why the correlation between A_{max} and $N\%$ or N_{area} is often not significant. For example, studies by Nagel and O'Hara (2001) and Porté and Loustau (1998) were performed in open canopy pine stands, in which little variation exists in LMA, and thus N_{area} (Porté and Loustau 1998). In contrast, studies that included a wide range in N_{area} (e.g., Bond et al. 1999) find quite a strong correlation with A_{max}. The varia-

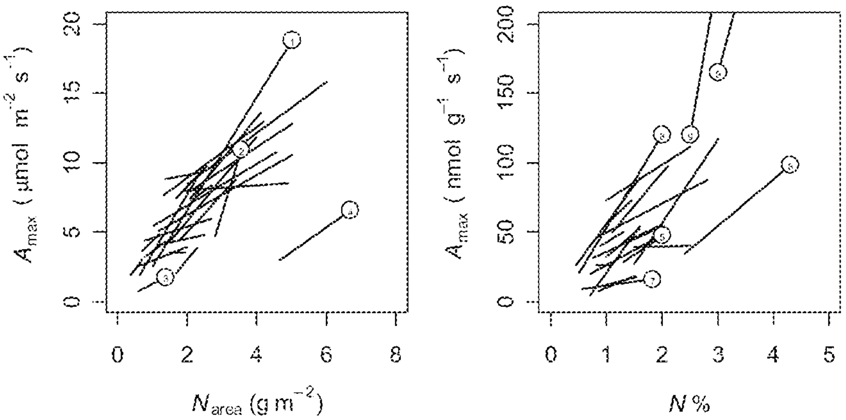

Figure 6. Comparison between light-saturated net photosynthetic rate (A_{max}) and area- and mass-based leaf nitrogen (N_{area} and $N\%$). Each line represents a study, or a relationship reported by a study. Each study was conducted on conifer species only. Selected studies are labeled: 1, Bond et al. 1999; 2, DeLucia and Schlesinger 1991 (across several species); 3, Schoettle and Smith 1998; 4, DeLucia and Schlesinger 1991 (across *Pinus monophylla* and *Juniperus osteosperma*); 5, Reich et al. 1995 (see also Aber et al. 1996); 6, Kloeppel et al. 2000; 7, Marshall et al. 1994 (*J. occidentalis*; a desert shrub); 8, Gower et al. 1993; and 9, Reich et al. 1998*b* (high-light and low-light grown seedlings separate; A_{max} increases to about 400 nmol g^{-1} s^{-1}).

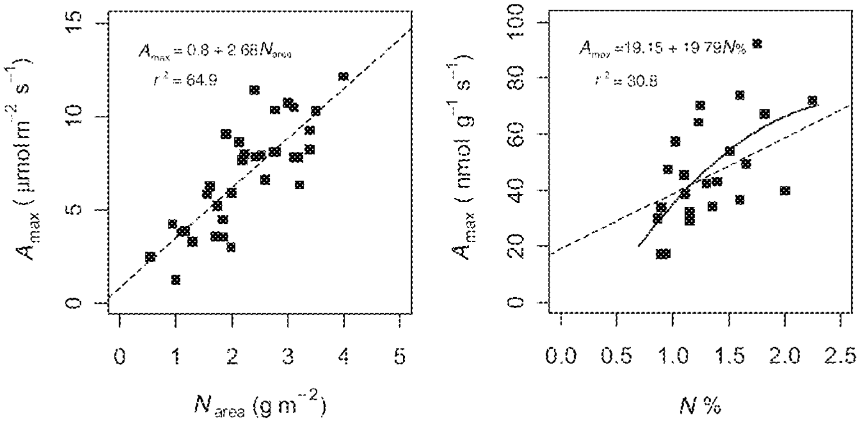

Figure 7. Comparison between light-saturated net photosynthetic rate (A_{max}) and area- and mass-based leaf nitrogen (N_{area} and $N\%$). Data are the same as in Figure 6, but only the midpoints of the lines are drawn, and the desert shrubs and the data of Reich et al. (1998*b*) are excluded because of their different nitrogen-use efficiencies. Each study was conducted on conifer species only. Dashed lines are least-squares regression lines. The solid line is a quadratic regression, which improved the fit slightly.

Table 6. Diagnostics for the linear regression of light-saturated assimilation rate (A_{max}) as a function of nitrogen content (N_{area}) or nitrogen concentration ($N\%$). The area-based comparison: A_{max}(area) = b_{0area} + $b_{1area}(N_{area})$ (r^2_{adj} = 64.9, RMSE = 1.67 μmol m^{-2} s^{-1}). Two equations are given for the mass-based comparison: A_{max}(mass) = b_{0mass} + $b_{1mass}(N\%)$ (r^2_{adj} = 27.8, RMSE = 16.32 nmol g^{-1} s^{-1}) and A_{max}(mass) = b_{0mass}' + $b_{1mass}'(N\%)$ + $b_{2mass}'(N\%)^2$ (r^2_{adj} = 37.2, RMSE = 14.9). The quadratic term was not significant for the area-based comparison. Sample sizes were 34 for the area-based comparison and 25 for the mass-based comparison.

Coefficient	Estimate	SE	$P(t_{obs} > \|t\|)$
b_{0area}	0.80	0.84	0.348
b_{1area}	2.68	0.35	< 0.0001
b_{0mass}	17.46	8.95	0.063
b_{1mass}	20.34	5.96	0.0024
b_{0mass}'	–23.95	22.15	0.29
b_{1mass}'	72.78	25.72	0.009
b_{2mass}'	–13.82	6.54	0.046

tion in the value for the slope of A_{max} versus N (i.e., N-use efficiency, NUE) can be explained likewise. If the range in $N\%$ or N_{area} is limited, a relatively large statistical uncertainty exists about the value of the slope, and multiple studies can therefore report different slopes as a result of random error in the slope estimate. For example, Vapaavuori (1995) found large variation in NUE during the seasons for *Pinus sylvestris* L., but could find no systematic changes in NUE.

A simple comparison of goodness of fit between area-based and mass-based comparisons showed that, across studies of conifer species, the area-based comparison resulted in a higher r^2 (64.9 versus 30.8%; Figure 7 and Table 6). Whether A_{max} and leaf N should be compared on an area or mass basis has been the topic of much debate (Field and Mooney 1986, Evans 1989, Reich and Walters 1994, Peterson et al 1999*a*). Field and Mooney (1986) found that, across non-evergreen species, the mass-based comparison gave a better fit. Reich et al. (1995, 1998*a*) reported that, across conifer species, area-based A_{max} was not correlated to N_{area}, but the mass-based comparison was significant. Our review revealed several studies reporting significant relationships between A_{max} and N_{area} in conifers. For example, Warren and Adams (2001) reported only area-based A_{max} and N because the mass-based comparison had a lower r^2 than the area-based comparison. On the other hand, if $N\%$ were relatively constant in a given population, there might still be a correlation between A_{max} and LMA, which several studies have found (e.g., Oren et al. 1986, Bond et al. 1999, Palmroth and Hari 2001, Robakowski et al. 2003). A third possible A_{max}–N relationship that has been analyzed is between area-based A_{max} and $N\%$ (e.g., Brix 1981, Smolander and Oker-Blom 1989, Green and Mitchell 1992).

The use of the photosynthesis–nitrogen relationship has been criticized (Woodward and Smith 1994) because there is a wide range of A_{max} values for a given value of N_{area} when all vegetation types are combined (see Evans 1989). However, this variance is greatly reduced when vegetation types are treated separately (see Field and Mooney 1986). Our review showed that, for the conifers as a collective, a strong general relationship exists, even though the methods, environmental variables and species varied among studies. We conclude that one photosynthesis–nitrogen relationship for conifers in coarsely aggregated models can be justified.

In conclusion, field sampling can be simplified by sampling the mean $N\%$, N_{area} and LMA halfway between the canopy top and the crown base. More research is needed, however, to demonstrate that these results are generally applicable. Neither the LAI of the stand, nor altitude, nor solar insolation had any effect on the canopy mean for these parameters, when averaged across species, except for the deciduous western larch. Species differed in $N\%$, LMA and N_{area}, indicating that species composition needs to be accounted for when parameterizing ecosystem models in mixed-species conifer forests. After accounting for species and topographic position, there was still considerable unexplained site variability. Light-saturated assimilation rate in conifers was correlated with leaf N, both in this study and in a review of the conifer literature. Stronger relationships were found for the area-based comparison than for the mass-based comparison. The use of one photosynthesis–nitrogen relationship for conifer species in coarse models is justified based on our study and a review of the conifer literature.

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Appendix

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Other studies included in the mass-based photosynthesis–nitrogen review

Brown et al. 1996, Kobayashi and Gyokusen 2002, Lusk et al. 2003, Matyssek and Schulze 1987, McKinnon and Mitchell 2003, Miller et al. 1991*a*, Miller et al. 1991*b*, Porté and Loustau 1998 (A. Porté, INRA Bordeaux, France, personal communication), Reich and Schoettle 1988, Reich et al. 1995 (see also Aber et al. 1996), Reich et al. 1998*a* (used data from Oleksyn et al. 1998), Vapaavuori et al. 1995, Warren and Adams 2000.