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Reconciling the apparent difference between mass- and area-based expressions of the photosynthesis-nitrogen relationship

Received: 7 May 1998 / Accepted: 19 October 1998

Abstract The relationship between photosynthetic carbon assimilation (A_{\max}) and leaf nitrogen content (N_{leaf}) can be expressed on either a leaf area basis (A_{area} vs N_{area}) or a leaf mass basis (A_{mass} vs N_{mass}). Dimensional analysis shows that the units for the slope of this relationship are the same for both expressions ($\mu\text{mol} [\text{CO}_2] \text{g}^{-1} [\text{N}] \text{s}^{-1}$). Thus the slope measures the change in CO_2 assimilation per gram of nitrogen, independent of leaf mass or leaf area. Although they have the same units, large differences between the area and mass-based slopes have been observed over a broad range of taxonomically diverse species. Some authors have claimed that regardless of these differences, the fundamental nature of the A_{\max} - N_{leaf} relationship is independent of the units of expression. In contrast, other authors have claimed that the area-based A_{\max} - N_{leaf} relationship is

fundamentally different from the mass-based relationship because of interactions between A_{\max} , N_{leaf} , and leaf mass per area (LMA, $\text{g} [\text{leaf}] \text{m}^{-2} [\text{leaf}]$). In this study we consider the mathematical relationships involved in the transformation from mass- to area-based expressions (and vice versa), and the implications this transformation has for the slope of the A_{\max} - N_{leaf} relationship. We then show that the slope of the relationship is independent of the units of expression when the effect of LMA is controlled statistically using a multiple regression. The validity of this hypothesis is demonstrated using 13 taxonomically and functionally diverse C_3 species. This analysis shows that the slope of the A_{\max} - N_{leaf} relationship is similar for the mass- and area-based expressions and that significant errors in the estimate of the slope can arise when the effect of LMA is not controlled.

Key words Photosynthesis · Leaf nitrogen · Leaf mass per area

CMEAL (CO₂ Models/Experiments Activity for improved Links) is a collaborative project aimed at improving the representation of CO₂ responses in ecosystem and global models.

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Introduction

The relationship between the light-saturated photosynthetic rate (A_{\max}) and leaf nitrogen content (N_{leaf}) has been studied extensively (e.g., Field and Mooney 1986; Walters and Field 1987; Evans 1989; Reich et al. 1994). This relationship is important for several reasons. First, A_{\max} tends to be positively correlated with N_{leaf} because the majority of leaf nitrogen is found in the proteins of the Calvin cycle (including Rubisco) and the thylakoid membranes (Evans 1989). Second, N_{leaf} can be used to estimate the maximum rate of carboxylation (V_{cmax}) and the light-saturated rate of electron transport (J_{max}) in the biochemical model of photosynthesis developed at Farquhar et al. (1980) because V_{cmax} is proportional to Rubisco content and J_{max} is proportional to the thylakoid protein content (Field 1983; Evans 1989; Harley et al. 1992). Third, the relationship between A_{\max} and N_{leaf} has been used to predict photosynthesis over scales ranging from the leaf to the globe (e.g., Aber and Fed-

erer 1992; Harley et al. 1992; Kirschbaum et al. 1994; Woodward and Smith 1994a,b; Aber et al. 1996). Fourth, the A_{\max} - N_{leaf} relationship has been implicated as evidence for global-scale convergent evolution of photosynthetic constraints (Reich et al. 1997; Reich et al. in press). The extent and diversity of studies of this relationship confirms its basic importance to our general understanding of plant biology.

The A_{\max} - N_{leaf} relationship is usually reported on either a leaf area basis (A_{area} , $\mu\text{mol} [\text{CO}_2] \text{m}^{-2} [\text{leaf}] \text{s}^{-1}$ and N_{area} , $\text{g} [\text{N}] \text{m}^{-2} [\text{leaf}]$) or a leaf mass basis (A_{mass} , $\mu\text{mol} [\text{CO}_2] \text{g}^{-1} [\text{leaf}] \text{s}^{-1}$ and N_{mass} , $\text{g} [\text{N}] \text{g}^{-1} [\text{leaf}]$). Dimensional analysis shows that the units for the slope of the A_{\max} - N_{leaf} relationship are the same for both expressions ($\mu\text{mol} [\text{CO}_2] \text{g}^{-1} [\text{N}] \text{s}^{-1}$) (see also Reich and Walters 1994). This is because the units for leaf area or leaf mass cancel when A_{\max} is divided by N_{leaf} . Thus the slope for both expressions represents the change in CO_2 assimilation per gram of nitrogen, independent of leaf mass or leaf area. Despite the fact that the slopes of the relationship for both expressions share the same units, substantial differences between the area-based slope (b_{area}) and the mass-based slope (b_{mass}) have been documented for a broad range of species (e.g., Field and Mooney 1986; Reich et al. 1992, 1994). Area-based relationships typically have lower correlations and lower slopes than the same data expressed on a mass basis. Field and Mooney (1986) and Evans (1989) concluded that even though these differences exist, the fundamental nature of the A_{\max} - N_{leaf} relationship is unaffected by the units of expression. In contrast, Reich et al. (1992) and Reich and Walters (1994) provide extensive data illustrating sometimes profound differences between b_{mass} and b_{area} for several taxonomically diverse species. Reich and Walters (1994, p. 80) state that "mass and area relations can not be assumed to be similar, or even easily comparable", and they conclude that the biological interpretation of these two coefficients is fundamentally different because "in reality they are measuring relationships of net carbon assimilation capacity and nitrogen contents along different leaf gradients" (Reich and Walters 1994, p. 81).

Are the mass and area-based expressions of the A_{\max} - N_{leaf} relationship fundamentally different? This question can be answered by examining the mathematical details of the transformation from mass-based to area-based expressions (or vice versa), and the implications this transformation has for the coefficients of the linear regression that is typically used to model the A_{\max} - N_{leaf} relationship. The transformation from mass- to area-based expressions of A_{\max} and N_{leaf} involves multiplying the mass-based expression by leaf mass per area (LMA, $\text{g} [\text{leaf}] \text{m}^{-2} [\text{leaf}]$), e.g., $A_{\text{area } i} = A_{\text{mass } i} \times \text{LMA}_i$, and $N_{\text{area } i} = N_{\text{mass } i} \times \text{LMA}_i$. If LMA were constant then this would be a linear transformation of both N_{mass} and A_{mass} . When variables are linearly transformed the coefficients obtained by regressing one variable on the other are also transformed according to specific rules. For the intercept (b_0) this transformation is $[b_0] = b_0 M_Y$,

and for the slope (b_1) it is $[b_1] = b_1 M_Y / M_X$ (Zar 1984, p. 290). In these two expressions M_X and M_Y are the constants that variables X and Y are multiplied by, respectively. The square brackets identify the transformed coefficients. If $M_Y = M_X$ then the ratio M_Y / M_X equals unity and $b_1 = [b_1]$, otherwise $b_1 \neq [b_1]$. The reason b_{area} does not usually equal b_{mass} is that LMA is not a constant but instead a random variable that tends to be inversely related to both A_{mass} and N_{mass} (e.g., Reich and Walters 1994; Reich et al. 1994). The transformation for $b_{0\text{mass}}$ to $b_{0\text{area}}$ can therefore be approximated as

$$b_{0\text{area}} = b_{0\text{mass}}(c - dA_{\text{mass}}) \quad (1)$$

and for $b_{1\text{mass}}$ to $b_{1\text{area}}$ as

$$b_{1\text{area}} = b_{1\text{mass}} \frac{c - dA_{\text{mass}}}{j - kN_{\text{mass}}} \quad (2)$$

where c and d are coefficients from the linear regression of LMA on A_{mass} , and j and k are coefficients from the linear regression of LMA on N_{mass} . The functional form of the relationship between LMA and A_{mass} , and between LMA and N_{mass} is not important for this argument. What is important in Eq. 2 is that the ratio of these functions (which must be unitless to be dimensionally correct) is unlikely to equal unity because A_{mass} and N_{mass} are measured using different units. Therefore $b_{1\text{area}}$ is unlikely to equal $b_{1\text{mass}}$.

To illustrate this point we calculated the coefficients c , d , j , and k for the deciduous tree *Betula pendula* grown in a controlled environment experiment (Rey and Jarvis 1998). These data gave the following ratio from Eq. 2:

$$\frac{76.72 - 82.37A_{\text{mass}}}{69.90 - 395.32N_{\text{mass}}}$$

This ratio is an increasing function of LMA and ranges from approximately 0.8 to approximately 1.15 (Fig. 1). This also explains the difference in the correlation between area- and mass-based expressions because $r = [r]$ when the variables are linearly transformed (Zar 1984, p. 290). Exactly how the transformation from mass to area-based expressions will affect $b_{1\text{area}}$ relative to $b_{1\text{mass}}$ will depend on the nature of the relationships in the numerator and denominator of Eq. 2. These relationships may be specific to the species or functional-type, and this may explain some of the variation in the photosynthesis-nitrogen relationship that has been observed across broad ranges of species (e.g., Evans 1989; Reich et al. 1995).

If we could control LMA so that it did not vary, then the ratio in Eq. 2 would equal unity and the regression functions would be unnecessary. We would then expect $b_{1\text{area}}$ to equal $b_{1\text{mass}}$. We can understand this intuitively by visualizing a hypothetical leaf of fixed dimensions and tissue density (i.e., fixed LMA). If we measured the rate of CO_2 uptake by the entire leaf and then replaced a fixed mass of nitrogen-deficient nonphotosynthetic tissue with the same mass of nitrogen-rich photosynthetic tissue without affecting the dimensions or density of the

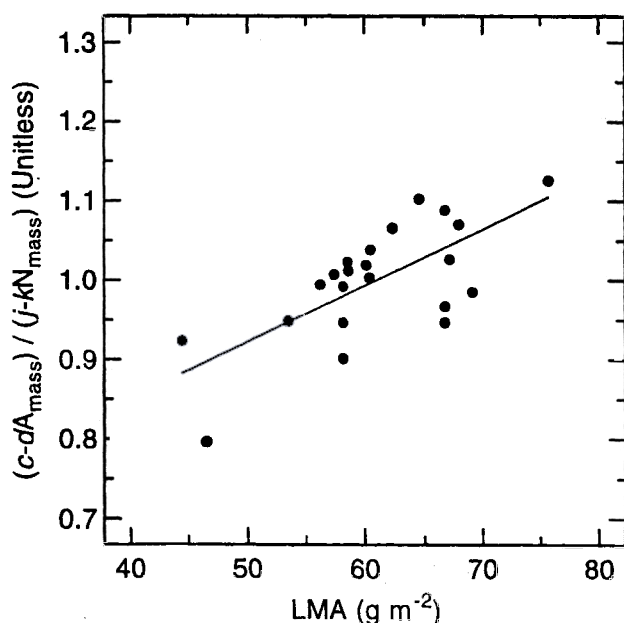


Fig. 1 The ratio $(c - dA_{\text{mass}})/(j - kN_{\text{mass}})$ from Eq. 2 versus LMA for *Betula pendula*

leaf, then the change in the rate of CO_2 uptake as a ratio of the change in the mass of nitrogen (i.e., the $A_{\text{max}}-N_{\text{leaf}}$ slope for both the area and the mass-based expressions) would be independent of the dimensions and density of the leaf because neither of these would have changed. In reality, though, controlling LMA experimentally is impractical, if not impossible, but we can control LMA statistically. The simplest way to do this is to use a linear multiple regression of A_{max} on N_{leaf} and LMA. We therefore hypothesize that the slope of the relationship between A_{max} and N_{leaf} will be similar for both area- and mass-based expressions when the effect of LMA is controlled using a multiple regression.

Methods

Data

All data used in this analysis were obtained from measurements on plants growing in natural environments or from controlled-environment experiments conducted in the field. There were a total of four species from field observations (one deciduous chaparral shrub, two evergreen shrubs and one evergreen tree) and nine woody species (two pines and seven deciduous trees) from controlled-environment experiments. Data consisted of rates of net photosynthetic carbon assimilation measured at light saturation under growth conditions (A_{area}), leaf nitrogen concentration (N_{mass}), and leaf mass per area (LMA). From these variables we calculated photosynthesis per leaf mass (A_{mass}) and nitrogen per leaf area (N_{area}). Nitrogen concentrations were usually determined from the same leaves on which photosynthesis was measured although in some cases adjacent leaves were collected for N analysis. Variations in N_{leaf} resulted from either fertilization treatments, differences between sun and shade leaves, leaf developmental stage, or natural variation within leaf classes (see the relevant citations for details). Photosynthesis measurements were made at ecologically relevant temperatures (20–30°C depending on species) and measurements for single species were usually controlled to within

$\pm 2^\circ\text{C}$. Measurements were made at ambient CO_2 concentration in the field, and CO_2 concentration in the controlled environment experiments was either 350 or 360 ppm (see the relevant citations for details).

Linear regressions

Leaf-level relationships between A_{max} , N_{leaf} and LMA were determined for the mass- and area-based expressions using least-squares multiple-regression. Least-squares regression is a valid technique when the independent variables are random (as in this analysis), as long as their frequency distributions are not functions of the regression coefficients (Neter et al. 1990, p. 86). We assumed that all data sets met this requirement.

The simple regression of A_{max} on N_{leaf} was determined using model 1, while model 2 was used to determine the multiple regression of A_{max} on N_{leaf} and LMA.

$$A_{\text{max}i} = b_0 + b_1 N_{\text{leaf}i} + \varepsilon_i \quad (\text{Model 1})$$

$$A_{\text{max}i} = b_0 + b_1 N_{\text{leaf}i} + b_2 \text{LMA}_i + \varepsilon_i \quad (\text{Model 2})$$

The important feature of model 2 is that the coefficients b_1 and b_2 are partial regression coefficients, meaning that they estimate the effect of one variable (either N_{leaf} or LMA) on A_{max} while the other variable is held constant. Models 1 and 2 were fitted to the area and mass-based data for each species. Comparison of b_1 from each model was made by subtracting $b_{1\text{mass}}$ from $b_{1\text{area}}$. 95% confidence intervals for coefficients, and the difference between $b_{1\text{area}}$ and $b_{1\text{mass}}$, were estimated by calculating the 2.5 and 97.5 percentiles obtained from 2000 bootstrap replicates (Efron and Tibshirani 1993). Bootstrapping involves resampling with replacement from the original data to simulate multiple samples from a population. It is useful when the statistical properties of the comparison being made are not well understood or require unreasonable assumptions, as is the case for our comparison of $b_{1\text{area}}$ and $b_{1\text{mass}}$. The bootstrap confidence intervals were not adjusted for comparisons across species and the reader is therefore discouraged from making such comparisons. In addition, the confidence intervals should be treated as approximate because some of the data sets were smaller than ideal for bootstrapping. Medians of the bootstrap distributions were reported instead of means because some distributions were highly skewed. Normality and homogeneity of residuals, and effects of multicollinearity were checked using the original non-bootstrapped data. Data for all species were pooled together and models 1 and 2 were fitted to the pooled data to test whether the hypothesis could be refuted at a hierarchical scale higher than a single species.

Determination of statistical significance

Statistical comparison of regression coefficients from each model was based on the bootstrap confidence intervals. Using this approach, two items are likely to be statistically different at the specified level of confidence when the confidence intervals for those items do not overlap. However, it is important to realize that the definitive test of whether those items are statistically different involves calculating the confidence interval for the difference between the two items as done for the comparison of regression coefficients discussed above. If this interval does not include zero then the items can be considered statistically different (Robinson 1982). Similarly, when the confidence intervals for two items do overlap this does not mean they are not significantly different. This can only be determined by calculating the confidence interval for their difference.

Results and discussion

There were noticeable differences between $b_{1\text{area}}$ and $b_{1\text{mass}}$ determined using model 1 for most species

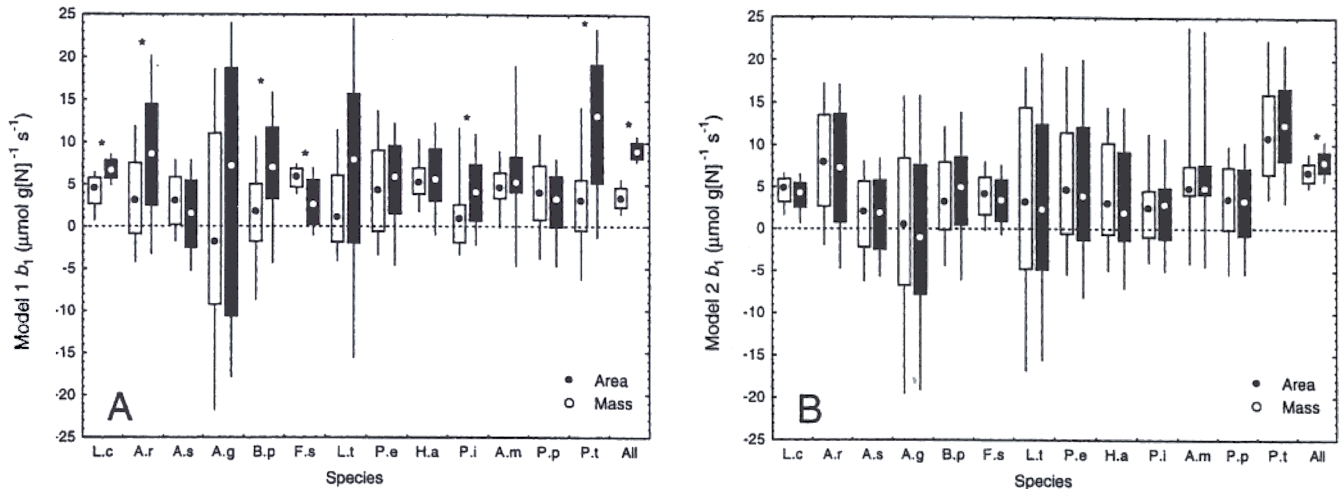


Fig. 2 A Median slope (b_1) of the A_{\max} - N_{leaf} relationship determined using model 1 for the area (●) and mass-based (○) expression. Boxes are the bootstrap 95% CI and whiskers are the range of the bootstrap distributions. Asterisks identify species that displayed significant or marginal differences between $b_{1\text{area}}$ and $b_{1\text{mass}}$ (see Fig. 3A for additional details). Initials on the x axis are species abbreviations (see below for details). B As for A but determined using model 2. [Species abbreviations and data citations: *L.c* *Lepichinia calycina* (deciduous chaparral shrub, Field and Mooney 1986), *A.r* *Acer rubrum* (deciduous tree, Norby et al. 1997), *A.s* *Acer saccharum* (deciduous tree, Norby et al. 1997), *A.g* *Alnus glutinosa* (nitrogen-fixing deciduous tree, Vogel and Curtis 1995), *B.p* *Betula pendula* (deciduous tree, Rey and Jarvis 1998), *F.s* *Fagus sylvatica* (deciduous tree, Forstreuter 1995), *L.t* *Liriodendron tulipifera* (deciduous tree, Gunderson and Wullschlegler 1994), *P.e* *Populus × euramericana* (deciduous tree, Curtis et al. 1995), *H.a* *Heteromeles arbutifolia* (evergreen shrub, Field and Mooney 1986), *P.i* *Prunus ilicifolia* (evergreen shrub, Field and Mooney 1986), *A.m* *Arbutus menziesii* (evergreen tree, Field and Mooney 1986), *P.p* *Pinus ponderosa* (evergreen tree, Tissue et al. in press), *P.t* *Pinus taeda* (evergreen tree, Tissue et al. 1997), All all species pooled]

(Fig. 2A). When the effect of LMA was controlled using model 2, essentially all differences between $b_{1\text{area}}$ and $b_{1\text{mass}}$ were removed for all 13 species (Fig. 2B). Under model 1, the difference between $b_{1\text{area}}$ and $b_{1\text{mass}}$ was significant for *L. calycina*, *B. pendula*, *P. taeda* and the pooled data set, and marginally significant for *A. rubrum* and *P. ilicifolia* (Fig. 3A). For each of these data sets, the median for $b_{1\text{mass}}$ tended to be higher than for $b_{1\text{area}}$. This difference was also marginally significant for *F. sylvatica*, but in this case $b_{1\text{area}}$ was higher than $b_{1\text{mass}}$.

When the effect of LMA was controlled using model 2, not only were the medians for $b_{1\text{area}}$ and $b_{1\text{mass}}$ made similar within species, but also the estimated 95% confidence intervals and the total range for each coefficient (Fig. 2B). The difference between $b_{1\text{area}}$ and $b_{1\text{mass}}$ under model 2 was not different from zero for all species, although some species were only marginally nonsignificant (Fig. 3A). Nevertheless, for those species that were marginally nonsignificant the observed difference between $b_{1\text{area}}$ and $b_{1\text{mass}}$ was small (Fig. 3A). The only exception was the pooled data set for which $b_{1\text{mass}}$ was still significantly larger than $b_{1\text{area}}$ although this difference was also small (Fig. 3A).

To determine if the difference between $b_{1\text{area}}$ and $b_{1\text{mass}}$ was larger for model 1 than for model 2, we subtracted the absolute value of this difference for model 2 from that for model 1, i.e., $|\text{model 1 } b_{1\text{area}} - b_{1\text{mass}}| - |\text{model 2 } b_{1\text{area}} - b_{1\text{mass}}|$. This comparison shows that the difference between $b_{1\text{area}}$ and $b_{1\text{mass}}$ was typically larger for model 1 than for model 2 (Fig. 3B). Although the significance of this comparison was marginal for most species, it does show a consistent trend for $b_{1\text{area}}$ and $b_{1\text{mass}}$ to be more similar under model 2 than under model 1.

We also compared b_1 from models 1 and 2 to see if model 1 under- or overestimated the slope of the A_{\max} - N_{leaf} relationship relative to model 2. This was done separately for the area and mass-based expressions by calculating $b_{1\text{model 1}} - b_{1\text{model 2}}$ and testing this difference against zero. There were statistically significant errors in the slope of the relationship given by model 1 relative to model 2 for *Lepichinia calycina*, *Acer rubrum*, *Pinus taeda* and the pooled data set, and marginally significant errors for *Betula pendula*, *Heteromeles arbutifolia* and *Prunus ilicifolia* (Fig. 4). For these species, $b_{1\text{area}}$ from model 1 generally underestimated the slope and/or $b_{1\text{mass}}$ from model 1 generally overestimated the slope. *Fagus sylvatica*, which displayed marginally significant errors, was an exception because its response was opposite to that of the species listed above. However, it is important to note that a significant difference between the area-based coefficients did not necessarily mean that the mass-based coefficients differed for that species and vice versa.

Species that displayed large or significant differences between $b_{1\text{area}}$ and $b_{1\text{mass}}$ under model 1 also displayed large or significant values for the partial regression coefficients for LMA from model 2 ($b_{2\text{area}}$ and $b_{2\text{mass}}$, Fig. 5). This supports the conclusion of Reich and Walters (1994) that LMA modifies the A_{\max} - N_{leaf} relationship through interactions with both photosynthesis and leaf nitrogen content. For those species that displayed significant values of $b_{2\text{area}}$ or $b_{2\text{mass}}$, an increase in LMA generally had a negative effect on A_{area} or A_{mass} when N_{leaf} was held constant. This negative association

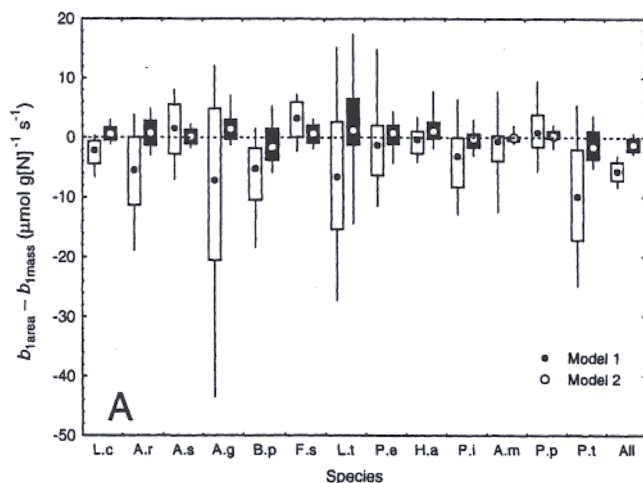


Fig. 3 A Median difference between the area- and mass-based expressions of the slope of the A_{\max} - N_{leaf} relationship (i.e., $b_{1\text{area}} - b_{1\text{mass}}$) determined using model 1 (●) and model 2 (○). All other details as for Fig. 1. **B** The difference between the absolute values for model 1 and model 2 shown in A, i.e., $|\text{model 1 difference}| - |\text{model 2 difference}|$

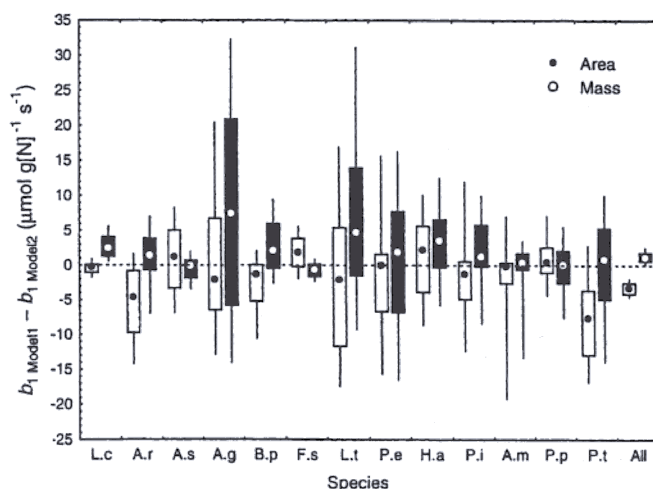
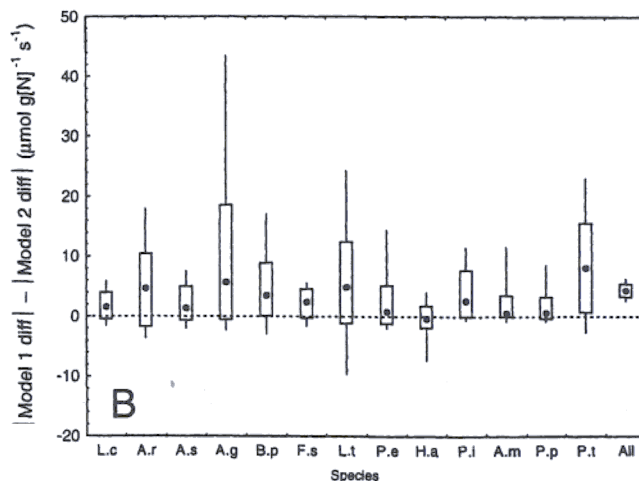


Fig. 4 Median difference between b_1 from models 1 and 2, i.e., $b_{1\text{model 1}} - b_{1\text{model 2}}$ for the area- (●) and mass-based (○) expressions. All other details as for Fig. 1

may be due to a reduction in nitrogen allocation to photosynthetic versus nonphotosynthetic compounds (Evans 1989), to greater allocation of biomass to structural versus photosynthetic components (Vitousek et al. 1990; Lloyd et al. 1992), to greater internal shading (Terashima and Hirotsuka 1995), or to greater limitations to internal diffusion (Parkhurst 1994).

The results of this analysis provide strong support for the hypothesis that the slope of the relationship between photosynthesis and leaf nitrogen content is fundamentally the same for both the area- and mass-based expressions when the effect of LMA is controlled statistically. Previously it had been suggested that the biological interpretation of $b_{1\text{area}}$ is fundamentally different to that of $b_{1\text{mass}}$ (Reich et al. 1992; Reich and

Walters 1994). This may be essentially true when the effect of LMA is not controlled. Reich and Walters (1994) correctly concluded that $b_{1\text{area}}$ differed from $b_{1\text{mass}}$ because of interactions between A_{\max} , N_{leaf} , and specific leaf area (SLA – the inverse of LMA). The current analysis extends that work by showing how these relationships are linked across units of expression and how those links tell us that $b_{1\text{area}}$ is expected to be fundamentally the same as $b_{1\text{mass}}$.

These results have several implications for physiological and ecological studies of photosynthesis. First, it confirms that the change in the rate of CO_2 assimilation as a function of leaf nitrogen content is independent of the units of expression when the effect of LMA is controlled. This is important because it shows that what was previously thought to be a complicated issue is in fact straightforward, and that the mathematical relationships involved are logical and robust. Second, it provides further evidence that LMA is an important regulator of photosynthesis although the mechanism of this effect is not well understood. Third, because of the dependencies between A_{\max} , N_{leaf} , and LMA, ecological studies of the A_{\max} - N_{leaf} relationship should control for potential effects of LMA. This may be particularly important in studies of patterns across species or functional types because LMA may confound results by biasing measures of central tendency and inflating variances.

This analysis also has important implications for models of leaf-level photosynthesis and plant growth. It shows that for some species statistically significant errors in the slope of the A_{\max} - N_{leaf} relationship occur when the effect of LMA is not controlled. Therefore it seems prudent to incorporate LMA into predictive models of photosynthesis. This should be mathematically simple, but it may complicate modeling efforts by increasing the amount of data needed to parameterize the models. Alternatively, modeling the A_{\max} - N_{leaf} relationship as a bivariate function of photosynthesis and leaf nitrogen content reduces the multidimensional response to a two-dimensional representation. The added accuracy that may be gained by treating the A_{\max} - N_{leaf} relationship as a multidimensional response may not, however, outweigh

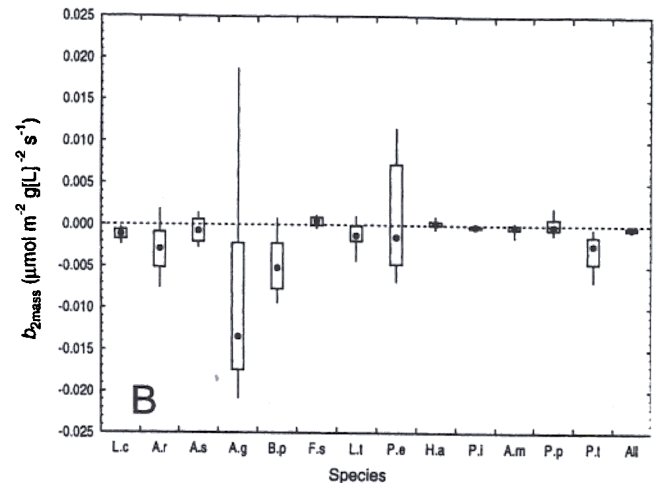
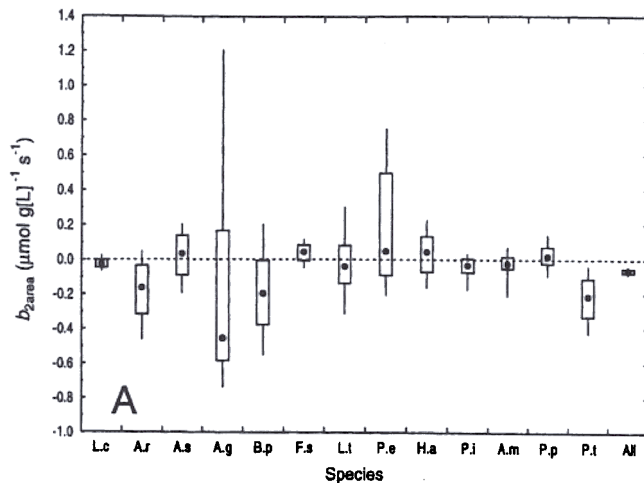


Fig. 5 Median slope of the relationship between photosynthesis and LMA (b_2) determined using model 2 for the A area- and B mass-based expressions. All other details as for Fig. 1

the difficulties in obtaining sufficient data to parameterize the models. There is a clear need for sensitivity analyses to determine how much LMA may affect model predictions. Nevertheless, if the aim of the models is to present and accurate mechanistic representation of photosynthesis then the results of this study reconcile some important misconceptions and help simplify the problem.

Acknowledgements This work was supported by the US Department of Energy, grant number DE-FG02-95ER62084 to the CMEAL (CO₂ Models/Experiments Activity for improved Links) program. The Electric Power Research Institute (EPRI) provided support for CMEAL meetings. Belinda Medlyn played an invaluable role in negotiating collaboration with members of the European collaboration on CO₂ Responses Applied to Forests and Trees (ECOCRAFT) program. Support for the initial organization of CMEAL was provided by the Desert Research Institute. Special thanks go to Peter Curtis, Christopher Field, Manfred Forstreuter, Kevin Griffin, Carla Gunderson, Richard Norby, Ana Rey, David Tissue, and Christoph Vogel for providing data. I also thank J. Timothy Ball, Yiqi Luo, Jim Coleman, Christopher Field, Kevin Griffin, Todd Dawson, and two anonymous reviewers for informed and helpful comments on an earlier version of this manuscript. CMEAL is a core project of the GCTE (Global Change and Terrestrial Ecosystems) program.

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