The photosynthesis - leaf nitrogen relationship at ambient and elevated atmospheric carbon dioxide: a meta-analysis

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Abstract

Estimation of leaf photosynthetic rate (A) from leaf nitrogen content (N) is both conceptually and numerically important in models of plant, ecosystem, and biosphere responses to global change. The relationship between A and N has been studied extensively at ambient CO_2 but much less at elevated CO_2. This study was designed to (1) assess whether the A-N relationship was more similar for species within than between community and vegetation types, and (2) examine how growth at elevated CO_2 affects the A-N relationship. Data were obtained for 39 C_3 species grown at ambient CO_2 and 10 C_3 species grown at ambient and elevated CO_2. A regression model was applied to each species as well as to species pooled within different community and vegetation types. Cluster analysis of the regression coefficients indicated that species measured at ambient CO_2 did not separate into distinct groups matching community or vegetation type. Instead, most community and vegetation types shared the same general parameter space for regression coefficients. Growth at elevated CO_2 increased photosynthetic nitrogen use efficiency for pines and deciduous trees. When species were pooled by vegetation type, the A-N relationship for deciduous trees expressed on a leaf-mass basis was not altered by elevated CO_2, while the intercept increased for pines. When regression coefficients were averaged to give mean responses for different vegetation types, elevated CO_2 increased the intercept and the slope for deciduous trees but increased only the intercept for pines. There were no statistical differences between the pines and deciduous trees for the effect of CO_2. Generalizations about the effect of elevated CO_2 on the A-N relationship, and differences between pines and deciduous trees will be enhanced as more data become available.

Introduction

Photosynthesis is the essential energy harvesting process for the total biosphere (Lange *et al.*, 1987) and therefore must be represented adequately in models of plant, ecosystem, and biosphere responses to global climate change. Both the light capture/electron transport and the carbon metabolism portions of photosynthesis require large investments of nitrogen in the form of proteins (Evans, 1989). The dependence of photosynthesis on nitrogenous compounds results in a general positive relationship between the light-saturated photosynthetic rate (A) and leaf nitrogen content (N) (Field and Mooney, 1986; Walters and Field, 1987; Evans, 1989; Reich *et al.*, 1994). This relationship, which is usually treated as linear, tends to be most clear when viewed across a broad range of species (e.g. Field and Mooney, 1986; Reich *et al.*, 1991a) but can be highly variable when individual species or narrow species groupings are compared (Evans, 1989; Sinclair and Horie 1989; Reich *et al.*, 1994; 1995). Despite this variation, the A-N relationship is an important component of predictive models of photosynthesis. It has been used as the conceptual (e.g. Woodward and Smith, 1994a,b) or numerical (e.g. Aber and Federer, 1992; Aber *et al.* 1996) basis for such models, and is related to the biochemical model of photosynthesis developed by Farquhar, von Caemmerer and Berry (1980) through the linear dependence of the maximum rate of carboxylation (Vc_{max}) and the light-saturated rate of electron transport (J_{max}) on leaf N (e.g. Harley *et al.* 1992; Kirschbaum *et al.* 1994).

The effect of elevated CO_2 on photosynthesis varies across species and experimental conditions (e.g. Luo *et al.*, 1994; Curtis, 1996). Nevertheless, long-term exposure to elevated CO_2 has been shown to reduce levels of Rubisco messenger RNA and subsequent enzyme concentrations (Krapp *et al.*, 1991; Stitt, 1991; Krapp *et al.*, 1993; Tissue, *et al.*, 1993), to alter the allocation of leaf N between Rubisco and electron transport components (Tissue *et al.* 1993), and to reduce the N concentration of leaf tissue (Luo *et al.*, 1994; Curtis, 1996). While some of these effects of elevated CO_2 may be regulated by nitrogen availability (McGuire *et al.*, 1995), they all have the potential to alter the A-N relationship relative to ambient CO_2. It is also possible that elevated CO_2 may affect the A-N relationship through interactions with other variables such as leaf mass per area. Some of these effects are represented in at least some ecosystem models, but none of the quantitative generalizations embodied in the models have been tested against data. This lack of empirical testing is a serious restriction for mechanistic models of ecosystem responses to global change (Kirschbaum, *et al.*, 1994; Woodward, *et al.*, 1995). In addition, our ability to generalize these effects of elevated CO_2 across multiple species in a way that is relevant to such models is even more restricted.

This study was designed to (1) assess whether the A-N relationship is more similar for species within than between community and vegetation types, and (2) examine how elevated CO_2 affects the A-N relationship. We used a combination of bivariate regression analysis and meta-analytic techniques to analyze the A-N relationship for 49 C_3 terrestrial plant species from field observations and field-based elevated CO_2 experiments.

Methods

Data

All data used in this analysis were obtained from measurements on plants growing in natural ecosystems, or from chamber-based elevated CO_2 experiments conducted in the field. There were 39 species from field observations and 10 woody species (three pines and seven deciduous trees) from CO_2 experiments (see Appendix for citations). Species were categorized by community type (e.g. successional, desert winter annuals, etc.) or by vegetation type (pines or deciduous trees). Community and vegetation types are referred to as groups for brevity. Data consisted of rates of net photosynthetic carbon assimilation (A_{area}, μmol [CO_2] m^{-2} [leaf] s^{-1}) measured at light saturation under growth conditions and operational levels of C_i, leaf nitrogen concentration (N_{mass}, g [N] g^{-1} [leaf]), and leaf mass per area (LMA, g [leaf] m^{-2} [leaf]). From these variables we calculated photosynthesis per leaf mass (A_{mass}, μmol [CO_2] g^{-1} [leaf] s^{-1}), and nitrogen per leaf area (N_{area}, g [N] m^{-2} [leaf]). In most data sets nitrogen concentration was determined using the same leaves that photosynthesis was measured on, although in some cases adjacent leaves were collected for N analysis. Causes of variation in leaf N differed across data sets and included fertilization treatments, sun vs. shade leaves, leaf developmental stage, and natural variation within leaf classes (see citations in Appendix for details). Photosynthesis measurements were made at ecologically relevant temperatures for each species (20 to 30°C depending on species), and measurements for single species were usually controlled to within ± 2°C. Ambient CO_2 concentration in the CO_2 experiments was either 350 or 360 ppm and the elevated concentration was either 650 or 700 ppm (see citations in Appendix for details).

Linear regressions

Leaf-level relationships between photosynthesis and leaf nitrogen content (both mass (A_{mass} vs. N_{mass}) and area (A_{area} vs. N_{area}) based) were determined using model I linear regression. The independent variables (N_{mass} and N_{area}) are random variables, but this does not present any problems with respect to linear regression as long as the frequency distribution of the independent variable is not a function of the regression coefficients (Neter *et al.*, 1990, pp. 86). We assumed that this was the case for all data sets in addition to accepting the standard assumptions of general linear models (Neter *et al.*, 1990, pp. 86 and 172). The basic assumptions of normality and homogeneity of variances were checked for all regressions using residual plots.

We present two different but complementary approaches to modeling the A-N relationship. In the first approach we fitted a single regression line to all data pooled together. This provides information on how photosynthesis changes across species with different leaf N contents and may be relevant to situations where changes in photosynthesis are driven by changes in species composition. We refer to this approach as the "pooled regression". Data were also pooled for each community and vegetation type to compare the A-N relationship across groups. The second approach used separate regressions for each species. The weighted average of each coefficient was calculated to give a mean and variance for each community and vegetation type. Weights were the inverse of each coefficient's variance, which is a function of the unexplained sum of squares and sample size. We refer to these averages as the "mean" or "averaged regressions", and they may be useful in situations where changes in photosynthesis are driven by changes in nitrogen availability for a particular community or vegetation type.

The linear model $Y_i = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \beta_3 X_{i1} X_{i2} + \varepsilon_i$ (Equation 1) was used to test for the effect of elevated CO_2 on the A-N relationship. In this model β_0 is the centered Y intercept for the ambient CO_2 treatment. Centering involves subtracting the grand mean of the independent variable (i.e., the mean for all species pooled together) from each data point, e.g. $N_{area\,i} - \overline{\overline{N}}_{area}$. This moves the Y axis to the grand mean of the independent variable and eliminates any uncertainty in the value of the intercept that results from extrapolating beyond the range of the data (Ryan, 1997, pp. 129). Values for the intercept at X = zero can be calculated by noting that $\overline{N}_{mass} = 0.017$ g g^{-1} and $\overline{N}_{area} = 1.305$ g m^{-2}. β_1 in Equation 1 is the slope for the ambient CO_2 treatment and β_2 is the change in the centered Y intercept due to elevated CO_2 (i.e., the intercept at elevated $CO_2 = \beta_0 + \beta_2$). β_3 (the interaction term) is the change in slope due to elevated CO_2, and the actual slope at elevated $CO_2 = \beta_1 + \beta_3$. X_{i1} is the independent variable and X_{i2} is a dummy variable coded as zero for ambient CO_2 and one for elevated CO_2 (Neter *et al*, 1990, pp. 356). This model was also used to test the robustness of the A-N relationship by comparing the relationship based on the data presented by Field and Mooney (1986) (the Vegetation In Natural Environments, or VINE data) with the relationship for all ambient CO_2 data combined. The combined data included the VINE data, additional field data, and ambient CO_2 treatment data from the CO_2 experiments. This comparison was made by fitting the model to all data pooled together with the dummy variable coded as zero for the VINE data treated as a separate group, and one for all data combined. Weighted least squares regression was used for this analysis because the error variance was positively correlated with the independent variable (Neter *et al.*, 1990, pp. 423).

Generalizing the A-N relationship within and between community and vegetation types

If regression coefficients were more similar within than between groups, then the accuracy of ecosystem and global models may be improved by incorporating specific details of different groups. We assessed the similarity of coefficients in two ways. First, we examined the distributional characteristics of the coefficients. This was done by treating each community and vegetation type as a separate population, and species within those groups were treated as random samples from those populations. Then for each group we compared the variance of the sample of coefficients to the variance expected if the population was normally distributed. If the observed and expected variances were similar then the sample was no more variable than would be expected from random sampling alone. On this basis we can classify the coefficients in that sample as being similar in magnitude. This was determined by calculating the ratio of the weighted sample-sum-of-squares and the sample variance (s^2) and comparing it to the χ^2 distribution with n-1 degrees of freedom (Hedges and Olkin, 1985). A nonsignificant result suggests that the coefficients were similar (statistically homogeneous), otherwise they were dissimilar (statistically heterogeneous). Weights were the inverse of each coefficient's variance.

Second, we used nonparametric hierarchical cluster analysis (Sokal and Rohlf, 1981; Digby and Kempton, 1987) on the regression coefficients from ambient CO_2 to gauge whether species within community and vegetation types formed discrete clusters. This would imply that the regression coefficients were more similar within than between groups. Coefficients were standardized to have a mean of zero and standard deviation of one, and the clustering criterion was complete linkage using Euclidean distances.

Statistical contrasts for the effect of elevated CO_2 on pines vs. deciduous trees

For the pooled regressions, Equation 1 was used to compare the A-N relationship for pines with that for deciduous trees at each CO_2 concentration. This was achieved by coding the dummy variable as zero for pines and one for deciduous trees.

For the mean regressions, the distribution of some of the coefficients from Equation 1 violated the assumptions of conventional parametric statistics (see results section for details). For this reason we used randomization tests (Manly, 1997) to compare the mean effect of elevated CO_2 on the A-N relationship for the pines with that for the deciduous trees. All comparisons were based on 5000 randomizations testing the null hypothesis that the observed mean difference between groups was a chance effect of observations taken in a random order. Although much still needs to be learned about how randomization tests are affected by non-normal and heteroscedastic data, these tests may be more powerful and robust than conventional parametric tests when data are less than ideal (Manly, 1997, pp. 80 and 98).

Results

The A-N relationship at ambient CO_2

Using the pooled regression for the VINE data expressed on a mass basis as a reference point, the additional ambient CO_2 data compiled here increased the noncentered intercept slightly but did not affect the slope of the A-N relationship (Table 1 and Figure 1). This indicates that the mass based relationship is both general and robust when multiple species are pooled together (regression analyses for each individual species are presented in the Appendix). In contrast, when the area based relationship was considered, the additional ambient CO_2 data did have a large effect on the VINE relationship. The additional data significantly reduced the noncentered intercept and significantly increased the slope (Table 1 and Figure 1).

The tests used to determine if species within groups had similar regression coefficients showed that species were dissimilar in all groups for the mass-based centered intercept at ambient CO_2 (Table 2). Nevertheless, there was strong evidence that species had similar slopes for the mass-based relationship at ambient CO_2 in each of the following groups: the deciduous trees and the pines from the CO_2 experiments, the evergreen shrubs, the old field annuals, the secondary successionals from the Amazonian Tierra Firme forests, the Amazonian pioneer species, and to a lesser extent the Amazonian late successionals from the Tierra Firme forests (Table 2). Species in the remaining five community types were dissimilar for the slope of the mass-based relationship at ambient CO_2 (Table 2). For the area-based expression of the A-N relationship, species were similar for the slope but not for the intercept in the old field annuals, the pioneers, the secondary successionals and the pines (Table 2). Species in all other groups were dissimilar for both the slope and the intercept expressed on an area basis (Table 2).

Hierarchical cluster analysis of the mass-based regression coefficients at ambient CO_2 did not separate species into discrete clusters matching the community or vegetation types presented in this study (hierarchical cluster trees not shown). Plotting the intercept coefficients against the slopes (Figure 2) shows little differentiation between groups. However, species in certain groups did appear to be clumped close together despite the lack of differentiation between groups (Figure 2), although this assessment may be considered somewhat subjective. Groups that appeared to cluster well were the old-field annuals, the secondary successionals, the late successionals, the deciduous trees and pines from the CO_2 experiments, and the deciduous trees from field observations. Within each of these groups (except the deciduous trees from field observations), species also had similar slope coefficients (see above), which supports the notion that these community and vegetation types do form clusters even though they may not be distinct from other groups. Broadly similar patterns were observed for the area-based cluster analysis (Figure 2) although the scatter appeared to be greater than for the mass-based analysis. Overall, the results of the cluster analyses suggest that many groups shared the same general parameter space for regression coefficients. The averaged regression coefficients for the community and vegetation types that appeared to cluster well are presented in Table 3.

Effect of elevated CO_2 on the A-N relationship for pines and deciduous trees

Pooled regressions - the response based on pooling species together

The mass-based regressions on the pooled data for the pines, and the pooled data for the deciduous trees, suggest that the centered intercepts for both vegetation types were similar at ambient CO_2 (Table 4 and Figure 3). The slope of the relationship at ambient CO_2 was 59% higher for the deciduous trees than for the pines, however, this difference was not significant (Table 4). Growth at elevated CO_2 appeared to increase the mass-based centered intercept for the deciduous trees but this was not significant (Table 4). Elevated CO_2 did increase the centered intercept for the pines by 50%, which was significant at a family-level confidence of 10%. This apparent difference between vegetation types for the effect of elevated CO_2 on the centered intercept was not significant (Table 4). Elevated CO_2 did not appear to affect the slope of the mass-based A-N relationship for either vegetation type, and there was no detectable difference between vegetation types for this response (Table 4).

The pooled regressions expressed on an area basis yielded a pattern of responses different from those discussed above. The centered intercept and slope for the deciduous trees at ambient CO_2 were, respectively, 72% and 280% higher than for the pines at ambient CO_2 (Table 4 and Figure 3). However, these differences were not significant due to the large variation in both A_{area} and N_{area}. Growth at elevated CO_2 did not affect the centered intercept for the pines, but did increase the centered intercept for the deciduous trees by 46%, which was significant at a family-level confidence of 5% (Table 4). Again, this apparent difference between vegetation types was not significant (Table 4). There was no evidence of a CO_2 effect on the slope of the area-based A-N relationship for either the pines or the deciduous trees, and no evidence of any difference between vegetation types for this response (Table 4).

Averaged regressions - the response based on averaging coefficients across species

The averaged regressions expressed on a mass basis suggest that growth at elevated CO_2 significantly increased the mean centered-intercept for both the pines (66%) and the deciduous trees (37%) at a family-level confidence of 10% (Table 5 and Figure 4). There was also evidence that elevated CO_2 significantly increased the mean slope of the mass-based relationship for the deciduous trees (41%), but not for the pines (Table 5). The randomization tests contrasting the means of each regression coefficient for the pines with those for the deciduous trees did not identify any significant differences between the two vegetation types at a family-level confidence of 10% (Table 5).

The averaged regressions expressed on an area basis indicate that growth at elevated CO_2 significantly increased the mean centered-intercept for both the pines (46%) and the deciduous trees (66%) (Table 5 and Figure 4). Elevated CO_2 also increased the mean slope of the area-based relationship by 87% for the deciduous trees, but had no significant effect on the mean slope for the pines (Table 5). Randomization tests did not identify any statistical differences between the pines and deciduous trees with regard to their area-based regression coefficients (Table 5).

The tests for similarity of regression coefficients suggest that species in both vegetation types were dissimilar for the effect of elevated CO_2 on the centered intercept of the mass-based A-N relationship (Table

2). Some of this variation within vegetation type may indicate species differences in the response of photosynthesis to elevated CO_2 at a given leaf nitrogen content, although some of the variation may also be due to other factors such as the seasonal timing of data collection, the temperature at which measurements were made, or to differences among experiments in the CO_2 concentration chosen for the elevated CO_2 treatment (650 vs. 700 ppm). Nevertheless, species in both of these vegetation types were similar for the effect of elevated CO_2 on the slope of the mass-based A-N relationship (Table 2). There was also strong evidence that the pines were similar for the effect of elevated CO_2 on the area-based intercept and slope, but the deciduous trees appeared to be dissimilar for both of these coefficients (Table 2).

General response to elevated CO_2

Because the comparisons of the pines and deciduous trees presented above did not identify any statistical differences between the two vegetation types, we combined both types into one group to generalize the effect of elevated CO_2 on the A-N relationship. Using the combined data, the pooled regression expressed on a mass basis showed that growth at elevated CO_2 significantly increased the centered intercept by 63%, but did not affect the slope of the relationship (Table 4). The area-based pooled-regression showed a similar pattern — growth at elevated CO_2 significantly increased the centered intercept by 48% and did not affect the slope (Table 4). The averaged regression for the mass-based expressions of A and N showed that elevated CO_2 significantly increased both the centered intercept (42%) and the slope (34%) of the relationship (Table 5). This general pattern was also found for the area-based averaged-regression, where growth at elevated CO_2 significantly increased the centered intercept by 59% and the slope by 74% (Table 5). The tests for homogeneity of the mass-based coefficients showed that the combined data were dissimilar for both intercept coefficients in Equation 1, but similar for both slope coefficients (Table 2). When these tests were performed on the combined data expressed on an area basis, all coefficients were dissimilar except the effect of elevated CO_2 on the slope (Table 2).

Discussion

The A-N relationship at ambient CO_2

This analysis showed that at ambient CO_2 the mass-based A-N relationship assessed by pooling across multiple community and vegetation types was general and robust – a finding that is consistent with previous studies (e.g., Reich, *et al.*, 1992; 1997). It is also clear from the rest of this analysis that plants do not simply move up and down the linear relationship in Figure 1 as nitrogen availability changes (see also Reich *et al.*, 1995; 1998a) or as atmospheric CO_2 concentration varies. Despite the strong positive correlation between photosynthesis and leaf N content viewed across many species, individual species do not always display an increase in photosynthesis with increasing leaf N content as the relationship in Figure 1 tends to suggest (see the Appendix for details). The data available to us indicate that the A-N relationship was highly variable across species, with more than an order of magnitude difference between certain species for the mass and area-based coefficients. Some of this variation in slope may be due to species differences in LMA because Reich *et al.* (1994; 1997; 1998a) have shown that for a given N_{mass} or range of N_{mass}, species with lower LMA have higher A_{mass} and a higher slope for the mass-based A-N relationship. Species specific differences in the proportional allocation of leaf nitrogen to photosynthetic and non-photosynthetic functions with increasing leaf nitrogen may also account for some of the variation in slope. Evans (1989) listed several possible explanations for variation in the intercept, including species specific differences in the total and relative allocation of leaf nitrogen to Rubisco and thylakoid proteins, differences in growth irradiance, and differences in stomatal conductance and consequently intercellular CO_2 concentrations.

The nature of the relationship between leaf nitrogen content and photosynthesis changed as one moved up hierarchies from single species to multiple community and vegetation types. These changes may have important implications for predictive models of photosynthesis. For example, the slope of the mass-based relationship pooled across all species (mean ± 95% c.i. = 9·83 ± 1·16) was greater than the weighted-average slope for all species (6·26 ± 0·057). Why do these differences exist? One possible explanation involves changes in the relationship between LMA and leaf N content, and between LMA and photosynthesis as additional species are pooled together. Variation in all three variables tends to be greater across species than within species (data not shown). Therefore the relationships between LMA, N, and photosynthesis may change as additional species are pooled together. Because of this, differences between the A-N relationship for the pooled regression versus the averaged regressions may be due, at least in part, to changes in the way that leaf N content and photosynthesis scale with LMA as additional species are pooled together (e.g. Reich *et al.* 1998a). If this is true, then differences in the A-N relationship between different hierarchical levels might be explained by simple changes in scaling relationships. Identifying these relationships could help us link the mechanisms of photosynthesis across different biological scales.

One aim of this study was to assess whether the A-N relationship was more similar for species within than between community and vegetation types. This information could be used to improve process-based biogeochemical models incorporating multiple species or communities. The cluster analyses and the distributional characteristics of the regression coefficients suggest that in approximately half the community and vegetation types represented here, species had similar A-N relationships. Thus, as a first approximation, the A-N relationship at ambient CO_2 may be generalized for each of the following community and vegetation types: the deciduous trees and pines from the CO_2 experiments, the old field annuals, the secondary successionals and late successionals from the Amazonian Tierra Firme forests, and the Amazonian pioneer species (see Table 3 for details). Even though the patterns of species groupings in this study were not distinct, Reich *et al.* (1995) present an example in which the A-N relationship pooled across species did discriminate clearly between deciduous hardwoods and evergreen conifers. Including additional variables such as LMA in analyses may help identify more robust and distinct groupings (e.g. Reich *et al.*, 1998a).

The regression coefficients for the pines and deciduous trees measured at ambient CO_2 in the CO_2 experiments were substantially higher than values reported by Reich *et al.* (1995) for naturally-grown adult deciduous hardwoods and evergreen conifers (comparisons not shown). In addition, our comparisons of the pines and deciduous trees from the CO_2 experiments did not identify any differences between these vegetation types at either ambient or elevated CO_2, whereas Reich *et al.* (1995) found distinctly different A-N responses for deciduous hardwoods and conifers at ambient CO_2. Part of the difference between the regressions reported here and those of Reich *et al.* (1995) may be due to different species combinations. For instance, both *Populus euramericana* and the nitrogen fixer *Alnus glutinosa* in the current data set have a large effect on the overall slope for the deciduous trees in the CO_2 experiments. Removing these species from the current study would tend to reduce the slope of the relationship, making it more similar to that of Reich *et al.* (1995). Additional variation may also be due to the age of the plants because trees in the CO_2 experiments were quite young and Reich *et al.* (1998b) found that the slope of the A-N relationship was typically higher for younger than for older trees.

Perhaps more importantly, the differences discussed above may reflect effects of experimental manipulations. In the natural environment, photosynthesis and the A-N relationship interact with, and are constrained by, multiple environmental variables (e.g. Field *et al.*, 1983; Fredeen, *et al.*, 1991). Many CO_2 chamber experiments are designed to examine a single variable (e.g. water or nitrogen) interacting with CO_2 while other potential resource limitations are either minimized or eliminated. These differences between the CO_2 chamber experiments and the natural A-N relationship suggest a need for multi-factorial experiments to assist the development of predictive models.

The A-N relationship at elevated CO_2

Growth at elevated CO_2 significantly increased photosynthetic nitrogen use efficiency for the pines and deciduous trees, but the nature of this effect depended on how the A-N relationship was modeled. For the pooled regressions, which show how photosynthesis changed across species with different leaf N content, the regression line for the elevated CO_2 data was offset vertically from the line for the ambient CO_2 data without affecting the slope. At a cursory level, this may be interpreted as meaning that the response of photosynthesis to elevated CO_2 may be predicted by simply extrapolating vertically from the ambient CO_2 line to the elevated CO_2 line. This would give the expected photosynthesis at elevated CO_2 for a given leaf N. However, elevated CO_2 also tends to decrease N_{mass} and increase N_{area} (Luo *et al.*, 1994; Curtis, 1996), so these adjustments need be taken into account to accurately predict the response for a particular species.

When the regression coefficients were averaged to give a mean and variance for each vegetation type, elevated CO_2 increased the centered intercept for the pines and deciduous trees, and increased the slope for the deciduous trees but not the pines. This difference between the pines and deciduous trees, while not statistically significant, may reflect larger interactions between CO_2 and LMA for the deciduous trees than for the pines. The extent to which LMA was responsible for the differences between the pooled and averaged regressions is not clear; but as discussed earlier, it may prove to be an important variable. Nevertheless, the observed differences between the pines and deciduous trees may be large enough to yield important differences in biogeochemical and biogeographic models. Sensitivity analyses exploring these potential differences are needed.

The two approaches used to model the A-N relationship (pooled and averaged regressions) produced different functional forms of the relationship. The choice of which approach to use in biogeochemical and biogeographic models depends on the questions being addressed, and the temporal and spatial scales being modeled. Use of the pooled regressions may be most appropriate when individual species are not the focus of interest. Such modeling scenarios may involve large spatial or temporal scales at which changes in photosynthesis are driven more by changes in dominant species composition than by changes in leaf N content of a single species. For example, a change in photosynthesis associated with a successional change in species could be modeled using the pooled regression presented in this paper. Regressions based on the averaged coefficients for a particular community or vegetation type may provide greater accuracy for modeling the response of photosynthesis over spatial or temporal scales at which species composition is not expected to change. For example, changes in photosynthesis for a mixed deciduous forest in response to changes in nitrogen availability could be simulated over periods of 50 to 100 years using the averaged regression for deciduous trees presented in this paper. This approach gives the typical relationship between photosynthesis and leaf N for a particular mixture of species, along with a measure of the variation in that relationship. There is clearly a need to determine how sensitive models are to these different representations of the A-N relationship. A judicious application of both approaches may provide a functionally important mechanism for adding realism to the competitive asymmetries among plants of different growth forms and from different biomes.

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Tables

Table 1. Pooled regression coefficients comparing the A-N relationship for the VINE data with that for the VINE data plus all additional ambient CO_2 data. Values are lower 95% c.i. < estimate < upper 95% c.i. Note: intercepts were not centered for this comparison.

Expression	VINE intercept	VINE slope	Effect of additional data on VINE intercept	Effect of additional data on VINE slope
Mass	-0·07 < -0·06 < -0·04 μmol g^{-1} s^{-1}	8·67 < 9·83 < 11·00 μmol g^{-1} s^{-1}	0·002 < 0·02 < 0·04 μmol g^{-1} s^{-1}	-2·42 < -1·18 < 0·07 μmol g^{-1} s^{-1}
Area	3·24 < 4·78 < 6·32 μmol m^{-2} s^{-1}	2·34 < 3·43 < 4·51 μmol g^{-1} s^{-1}	-6·35 < -4·73 < -3·10 μmol m^{-2} s^{-1}	1·31 < 2·50 < 3·70 μmol g^{-1} s^{-1}

Table 2. Chi-square *P* values for tests of similarity of regression coefficients within community and vegetation types. A nonsignificant value suggests similarity.

Design	Community or vegetation type	N	Mass based expression				Area based expression			
			Centered intercept at ambient CO_2	Slope at ambient CO_2	Effect of elevated CO_2 on centered intercept	Effect of elevated CO_2 on slope	Centered intercept at ambient CO_2	Slope at ambient CO_2	Effect of elevated CO_2 on centered intercept	Effect of elevated CO_2 on slope
Field	Death Valley annual	2	< 0·001	< 0·001			0·549	< 0·001		
Field	Deciduous tree	3	< 0·001	< 0·001			< 0·001	< 0·001		
Field	Evergreen shrub	3	< 0·001	0·976			< 0·001	< 0·001		
Field	Evergreen tree	2	< 0·001	< 0·001			< 0·001	< 0·001		
Field	Late successional (Bana)	5	< 0·001	< 0·001			< 0·001	< 0·001		
Field	Late successional (Caatinga)	5	< 0·001	0·005			< 0·001	< 0·001		
Field	Late successional (Tierra Firme)	5	< 0·001	0·061			< 0·001	< 0·001		
Field	Old field annual	4	< 0·001	0·953			< 0·001	0·367		
Field	Pioneer	2	< 0·001	0·817			0·021	0·722		
Field	Secondary successional (Tierra Firme)	5	< 0·001	0·413			< 0·001	0·368		
CO_2	Pine	3	< 0·001	0·750	< 0·001	0·869	< 0·001	0·813	0·324	0·907
CO_2	Deciduous tree	7	< 0·001	0·996	< 0·001	0·998	< 0·001	< 0·001	< 0·001	0·098
Field	All species	39	< 0·001	< 0·001			< 0·001	< 0·001		
CO_2	All species	10	< 0·001	0·999	< 0·001	1·000	< 0·001	< 0·001	< 0·001	0·229

Table 3. Averaged regression coefficients for the community and vegetation types that appeared to group well at ambient CO_2 on the basis of tests for similarity of coefficients and cluster analyses. P values for heterogeneous coefficients are approximate (denoted by ≈).

Community or vegetation type	Centered intercept at ambient CO_2 ± s.e.	Slope at ambient CO_2 ± s.e.
Mass based expressions		
	$\mu mol\ g^{-1}\ s^{-1}$	$\mu mol\ g^{-1}\ s^{-1}$
Late successional Tierra Firme	0·059 ± 0·002 ($P \approx$ 0·001)	3·741 ± 0·674 (P = 0·001)
Old field annuals	0·188 ± 0·026 ($P \approx$ 0·001)	6·809 ± 1·882 (P = 0·005)
Amazonian pioneer	0·161 ± 0·025 ($P \approx$ 0·069)	7·477 ± 3·366 (P = 0·196)
Secondary successional Tierra Firme	0·121 ± 0·003 ($P \approx$ 0·001)	11·941 ± 0·692 (P = 0·001)
Deciduous trees (CO_2 experiments)	0·115 ± 0·005 ($P \approx$ 0·001)	4·604 ± 1·096 (P = 0·001)
Pines (CO_2 experiments)	0·093 ± 0·009 ($P \approx$ 0·003)	7·070 ± 1·891 (P = 0·023)
Area based expressions		
	$\mu mol\ m^{-2}\ s^{-1}$	$\mu mol\ g^{-1}\ s^{-1}$
Late successional Tierra Firme	4·451 ± 0·125 ($P \approx$ 0·001)	3·206 ± 0·285 ($P \approx$ 0·001)
Old field annuals	12·544 ± 0·849 ($P \approx$ 0·001)	6·946 ± 1·247 (P = 0·002)
Amazonian pioneer	12·717 ± 1·234 ($P \approx$ 0·044)	5·764 ± 2·904 (P = 0·014)
Secondary successional Tierra Firme	9·053 ± 0·343 ($P \approx$ 0·001)	8·373 ± 0·942 (P = 0·001)
Deciduous trees (CO_2 experiments)	7·769 ± 0·265 ($P \approx$ 0·001)	4·644 ± 0·622 ($P \approx$ 0·001)
Pines (CO_2 experiments)	7·285 ± 0·370 ($P \approx$ 0·001)	3·551 ± 1·198 (P = 0·036)

Table 4. Pooled regression coefficients testing the effect of elevated CO_2 on the A-N relationship for pines and deciduous trees. A Bonferroni-adjusted *P* value of 0·025 is significant at a family-level confidence of 10%.

Tree type	R^2	Centered intercept at ambient CO_2 ± s.e.	Slope at ambient CO_2 ± s.e.	Effect of elevated CO_2 on centered intercept ± s.e.	Effect of elevated CO_2 on slope ± s.e.
Mass based expression					
		μmol g^{-1} s^{-1}	μmol g^{-1} s^{-1}	μmol g^{-1} s^{-1}	μmol g^{-1} s^{-1}
Pines	0·990	0·110 ± 0·004 ($P = 0·001$)	9·046 ± 1·100 ($P = 0·014$)	0·055 ± 0·007 ($P = 0·014$)	1·600 ± 1·587 ($P = 0·420$)
Deciduous	0·784	0·094 ± 0·029 ($P = 0·009$)	15·246 ± 4·017 ($P = 0·004$)	0·075 ± 0·037 ($P = 0·066$)	4·311 ± 6·028 ($P = 0·491$)
P value for difference between pines and deciduous		0·648	0·385	0·904	0·390
Pines & deciduous combined	0·821	0·109 ± 0·015 ($P < 0·001$)	13·146 ± 2·389 ($P < 0·001$)	0·069 ± 0·020 ($P = 0·003$)	3·859 ± 3·656 ($P = 0·307$)
Area based expression					
		μmol m^{-2} s^{-1}	μmol g^{-1} s^{-1}	μmol m^{-2} s^{-1}	μmol g^{-1} s^{-1}
Pines	0·940	7·445 ± 0·613 ($P = 0·007$)	4·352 ± 2·335 ($P = 0·203$)	4·704 ± 1·892 ($P = 0·131$)	5·371 ± 6·866 ($P = 0·516$)
Deciduous	0·915	10·400 ± 1·044 ($P < 0·001$)	12·194 ± 2·397 ($P < 0·001$)	4·773 ± 1·475 ($P = 0·009$)	3·925 ± 3·073 ($P = 0·230$)
P value for difference between pines and deciduous		0·146	0·265	0·711	0·826
Pines & deciduous combined	0·912	9·974 ± 0·753 ($P < 0·001$)	12·186 ± 1·923 ($P < 0·001$)	4·827 ± 1·066 ($P < 0·001$)	4·278 ± 2·487 ($P = 0·105$)

Table 5. Averaged regression coefficients testing the effect of elevated CO_2 on the A-N relationship for deciduous trees and pines. *P* values for heterogeneous coefficients are approximate (denoted by ≈). A Bonferroni-adjusted *P* value of 0·025 is significant at a family-level confidence of 10%.

Tree type	Centered intercept at ambient CO_2. Weighted mean ± s.e. of sample	Slope at ambient CO_2. Weighted mean ± s.e. of sample	Effect of elevated CO_2 on centered intercept. Weighted mean ± s.e. of sample	Effect of elevated CO_2 on slope. Weighted mean ± s.e. of sample
Mass based expression				
	μmol g^{-1} s^{-1}	μmol g^{-1} s^{-1}	μmol g^{-1} s^{-1}	μmol g^{-1} s^{-1}
Pine	0·093 ± 0·009 ($P \approx 0·003$)	7·070 ± 1·891 ($P = 0·023$)	0·061 ± 0·013 ($P \approx 0·015$)	1·327 ± 2·846 ($P = 0·504$)
Deciduous	0·115 ± 0·005 ($P \approx 0·001$)	4·604 ± 1·096 ($P < 0·001$)	0·043 ± 0·007 ($P \approx 0·001$)	1·898 ± 1·550 ($P = 0·018$)
P value for difference *between pines and* deciduous	0·066	0·468	0·442	0·892
Pines & deciduous combined	0·111 ± 0·004 ($P \approx 0·001$)	5·224 ± 0·948 ($P < 0·001$)	0·047 ± 0·006 ($P \approx 0·001$)	1·768 ± 1·361 ($P = 0·003$)
Area based expression				
	μmol m^{-2} s^{-1}	μmol g^{-1} s^{-1}	μmol m^{-2} s^{-1}	μmol g^{-1} s^{-1}
Pine	7·285 ± 0·370 ($P \approx 0·001$)	3·551 ± 1·198 ($P = 0·036$)	3·323 ± 0·539 ($P = 0·009$)	0·732 ± 1·656 ($P = 0·524$)
Deciduous	7·769 ± 0·268 ($P \approx 0·001$)	4·644 ± 0·622 ($P \approx 0·001$)	5·154 ± 0·405 ($P \approx 0·001$)	4·038 ± 0·901 ($P \approx 0·001$)
P value for difference between pines and deciduous	0·546	0·796	0·226	0·294
Pines & deciduous combined	7·605 ± 0·215 ($P \approx 0·001$)	4·412 ± 0·552 ($P \approx 0·001$)	4·495 ± 0·324 ($P \approx 0·001$)	3·283 ± 0·791 ($P < 0·001$)

Figure legends

Figure 1. A-N relationships at ambient CO_2 for all species pooled together and expressed on a mass basis (panel A) and an area basis (panel B). Points are the mean for each community or vegetation type. Error bars have been omitted for clarity. Largest standard errors were 0·002 for N_{mass}, 0·03 for A_{mass}, 0·2 for N_{area}, and 1·9 for A_{area}. The solid lines are the pooled regressions for the VINE data and the dashed lines are the pooled regressions for all ambient CO_2 data including the VINE data and CO_2 experiment data. Abbreviations: Amaz = Amazonian; DC = deciduous chaparral; DT = deciduous tree; DV = Death Valley; EG = Evergreen; LS = late successional; MS = mid successional; OF = old field; SS = secondary successional.

Figure 2. Intercept vs. slope for the mass-based (panel A) and area-based (panel B) regressions. Points are the coefficients for each species identified by community or vegetation type. Coefficients were standardised to have a mean of zero and standard deviation of one to remove the effects of different scales on the *X* and *Y* axes. Abbreviations as for Figure 1.

Figure 3. Pooled regressions for the effect of elevated CO_2 on the A-N relationship for pines (▲) and deciduous trees (●) expressed on a mass basis (panel A) and on an area basis (panel B). Closed symbols = ambient CO_2, open symbols = elevated CO_2. Points are the mean for each species at each CO_2 concentration. Error bars have been omitted for clarity. Largest standard errors were 0·003 for N_{mass}, 0·03 for A_{mass}, 0·15 for N_{area}, and 1·5 for A_{area}. The dashed vertical lines mark the location of the centered intercepts (0·017 for N_{mass} and 1·305 for N_{area}).

Figure 4. Averaged regressions for the effect of elevated CO_2 on the A-N relationship for pines (thick lines) and deciduous trees (thin lines) expressed on a mass basis (panel A) and on an area basis (panel B). Closed symbols and solid lines = ambient CO_2, open symbols and dashed lines = elevated CO_2. Points are the mean for each species. Error bars have been omitted for clarity. Largest standard errors were 0·003 for N_{mass}, 0·03 for A_{mass}, 0·15 for N_{area}, and 1·5 for A_{area}. Note that the regression lines are the weighted average regressions and were not calculated directly from the points in the figure. The dashed vertical lines mark the location of the centered intercepts (0·017 for N_{mass} and 1·305 for N_{area}).

Figures

Figure 1

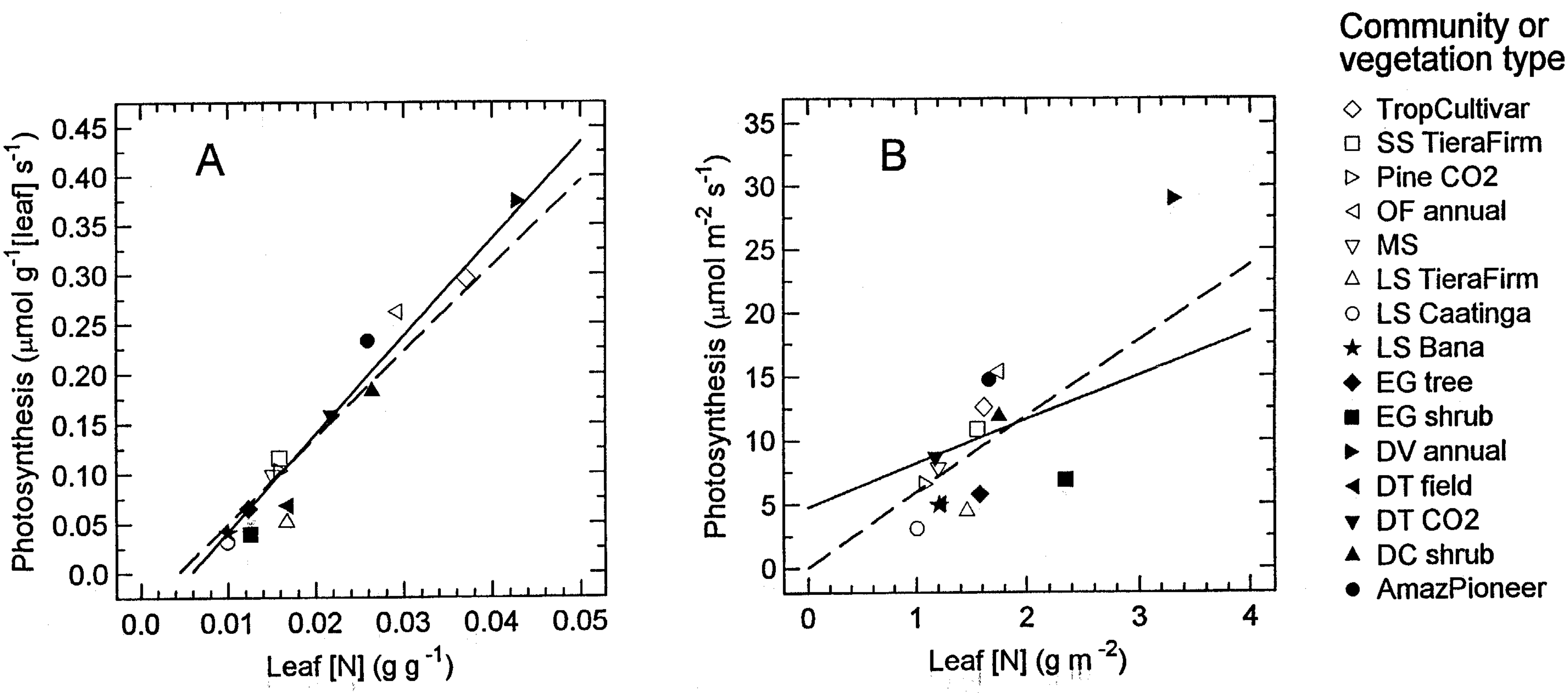


Figure 2

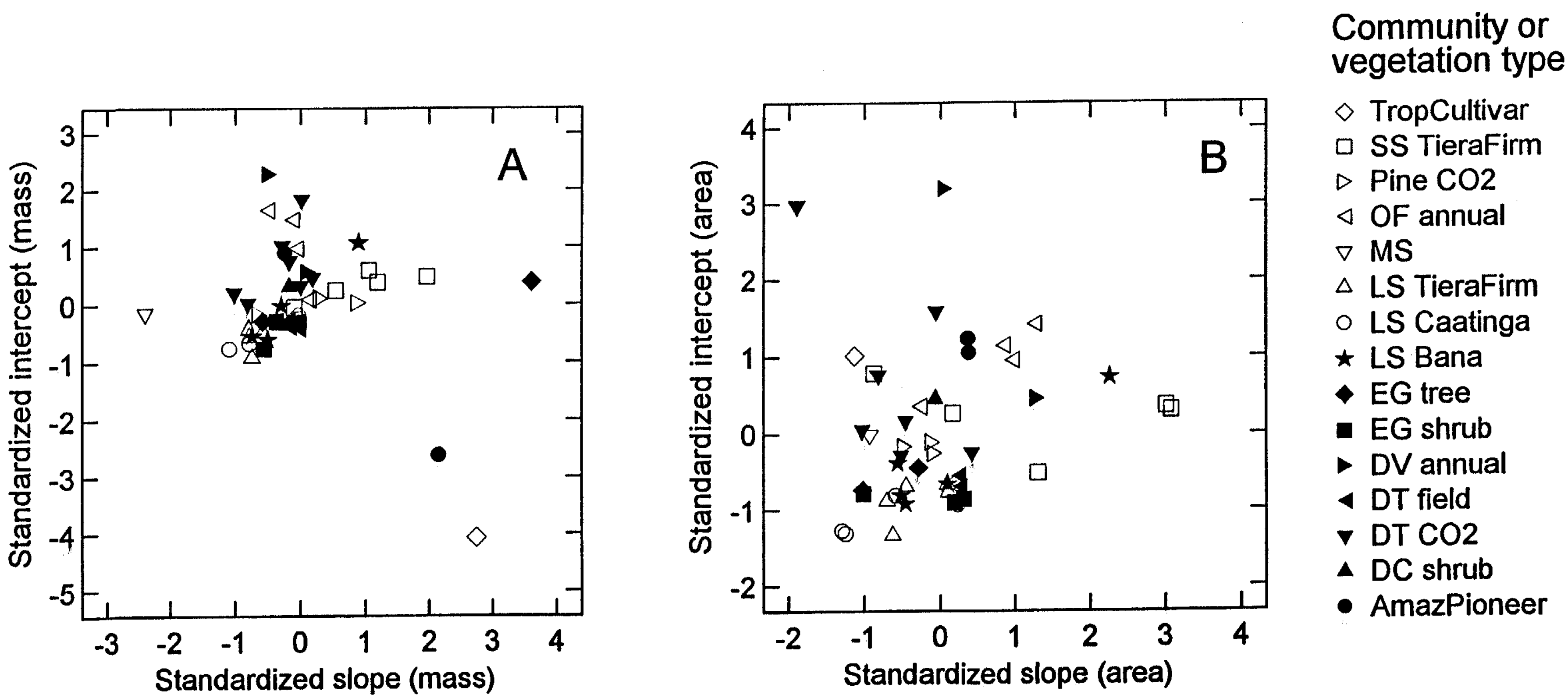

A
Standardized intercept (mass)
Standardized slope (mass)
3
2
1
0
-1
-2
-3
-4
-5
-3
-2
-1
0
1
2
3
4
B
Standardized intercept (area)
Standardized slope (area)
4
3
2
1
0
-1
-2
-2
-1
0
1
2
3
4
Community or vegetation type
TropCultivar
SS TieraFirm
Pine CO2
OF annual
MS
LS TieraFirm
LS Caatinga
LS Bana
EG tree
EG shrub
DV annual
DT field
DT CO2
DC shrub
AmazPioneer

Figure 3

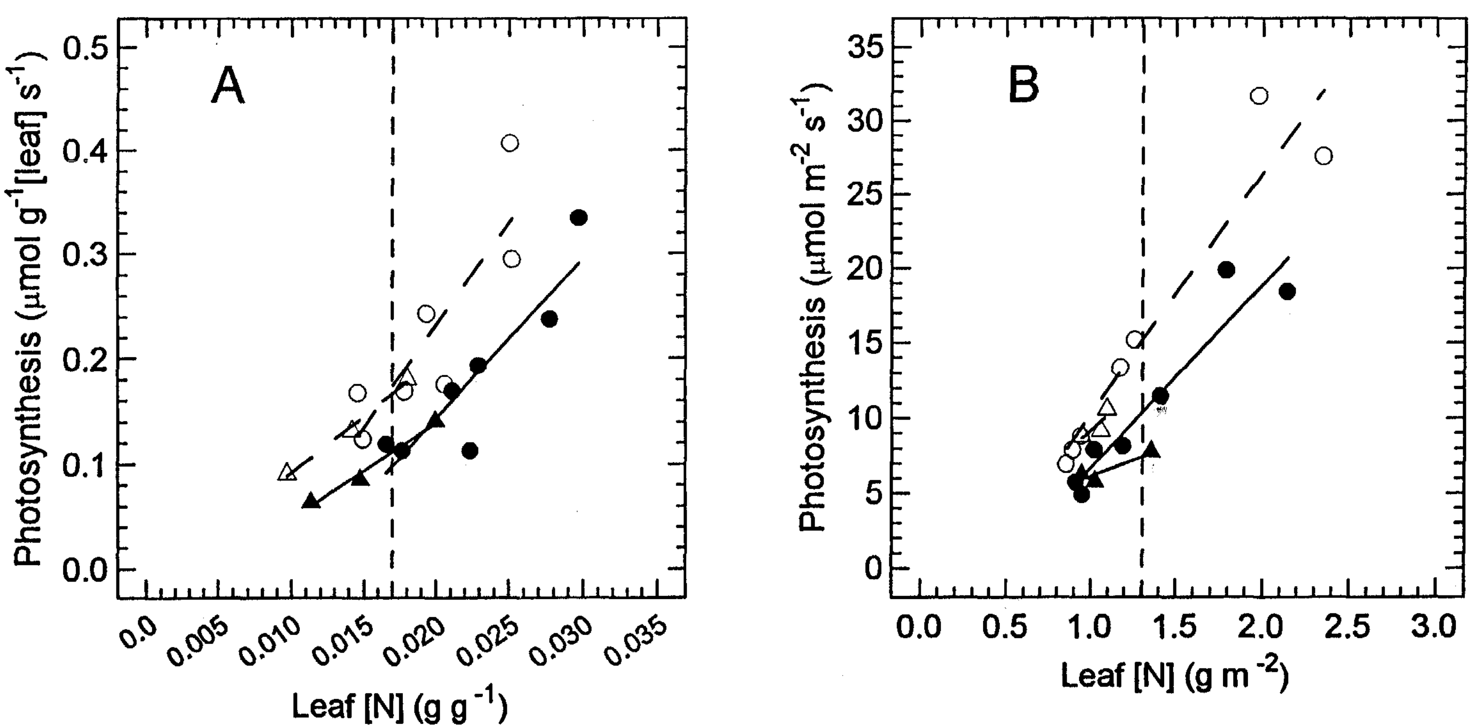
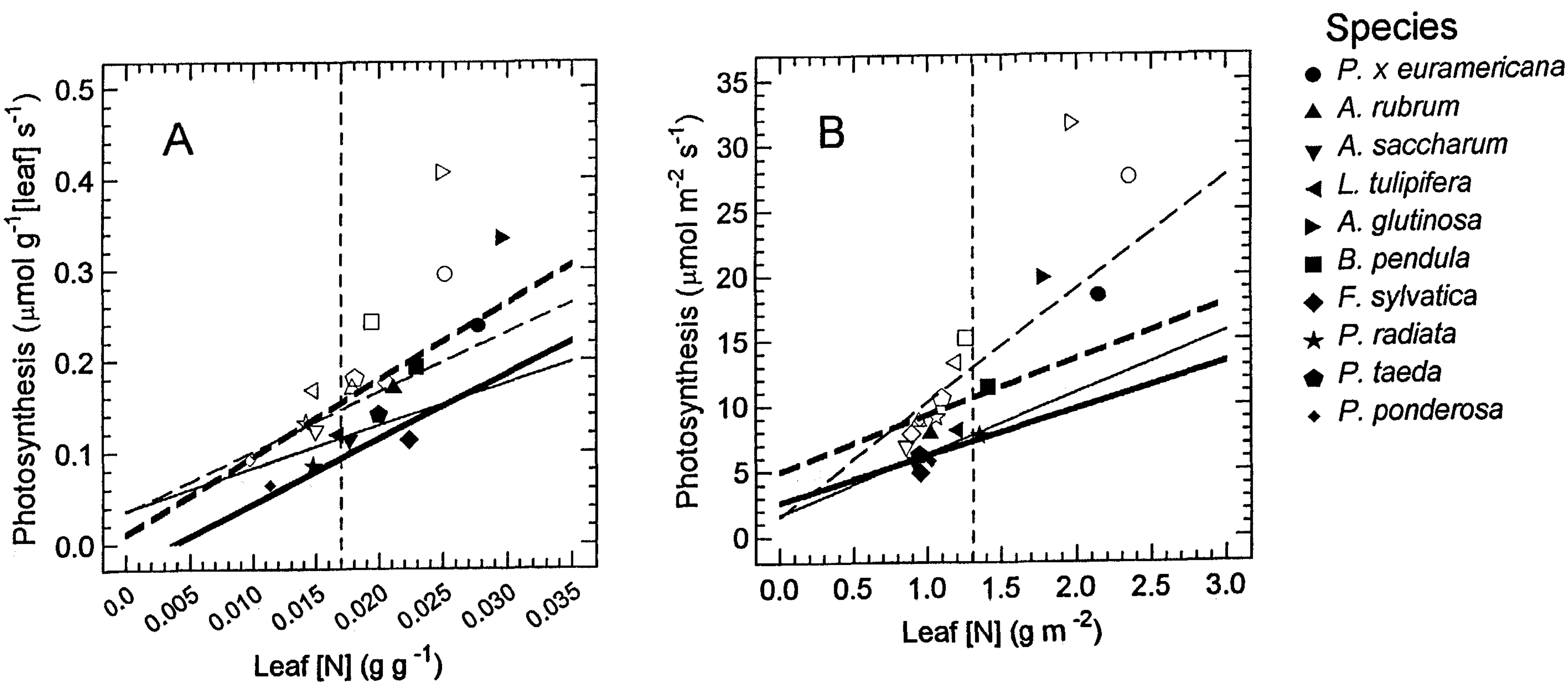

A
B
Photosynthesis (μmol g-1[leaf] s-1)
0.0
0.1
0.2
0.3
0.4
0.5
0.0
0.005
0.010
0.015
0.020
0.025
0.030
0.035
Leaf [N] (g g -1)
Photosynthesis (μmol m-2 s-1)
0
5
10
15
20
25
30
35
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Leaf [N] (g m -2)

Figure 4.


A
Photosynthesis (µmol g⁻¹[leaf] s⁻¹)
0.0
0.1
0.2
0.3
0.4
0.5
0.0
0.005
0.010
0.015
0.020
0.025
0.030
0.035
Leaf [N] (g g⁻¹)
B
Photosynthesis (µmol m⁻² s⁻¹)
0
5
10
15
20
25
30
35
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Leaf [N] (g m⁻²)
Species
P. x euramericana
A. rubrum
A. saccharum
L. tulipifera
A. glutinosa
B. pendula
F. sylvatica
P. radiata
P. taeda
P. ponderosa

Appendix. Table A1. Results for the mass and area-based regressions for individual species from the field observations. Citations are: 1 = Field and Mooney (1986); 2 = Reich *et al.* (1991b); 3 = Reich *et al.* (1994).

			Mass based expression			Area based expression		
Community or vegetation type and citation number	Species	N	R^2	Centered intercept ± s.e. (P value) µmol g^{-1} s^{-1}	Slope ± s.e. (P value) µmol g^{-1} s^{-1}	R^2	Centered intercept ± s.e. (P value) µmol m^{-2} s^{-1}	Slope ± s.e. (P value) µmol g^{-1} s^{-1}
Death Valley annual 1	*Abronia villosa*	4	0·619	0·268 ± 0·062 (0·049)	4·609 ± 2·555 (0·213)	0·547	21·634 ± 6·142 (0·072)	4·673 ± 3·007 (0·260)
	Gerea canescens	7	0·916	0·139 ± 0·033 (0·009)	8·381 ± 1·135 (0·001)	0·908	9·952 ± 2·646 (0·013)	8·815 ± 1·252 (0·001)
Deciduous chaparral shrub 1	*Lepechinia calycina*	30	0·810	0·120 ± 0·008 (< 0·001)	6·546 ± 0·600 (< 0·001)	0·521	9·938 ± 0·479 (< 0·001)	4·269 ± 0·773 (< 0·001)
Deciduous tree 2	*Acer rubrum*	28	0·758	0·076 ± 0·003 (< 0·001)	6·416 ± 0·712 (< 0·001)	0·704	5·672 ± 0·265 (< 0·001)	5·320 ± 0·677 (< 0·001)
	Acer saccharum	81	0·745	0·068 ± 0·002 (< 0·001)	6·534 ± 0·430 (< 0·001)	0·750	5·690 ± 0·179 (< 0·001)	5·324 ± 0·346 (< 0·001)
	Quercus ellipsoidalis	33	0·538	0·066 ± 0·005 (< 0·001)	7·457 ± 1·240 (< 0·001)	0·565	5·065 ± 0·696 (< 0·001)	5·377 ± 0·847 (< 0·001)
Evergreen shrub 1	*Prunus ilicifolia*	10	0·647	0·039 ± 0·003 (< 0·001)	4·110 ± 1·073 (0·005)	0·163	4·688 ± 1·860 (0·036)	1·107 ± 0·887 (0·247)
	Heteromeles arbutifolia	12	0·666	0·075 ± 0·010 (< 0·001)	5·315 ± 1·191 (0·001)	0·841	4·165 ± 0·530 (< 0·001)	5·140 ± 0·708 (< 0·001)
	Rhamnus californica	6	0·865	0·073 ± 0·006 (< 0·001)	7·461 ± 1·473 (0·007)	0·570	4·378 ± 1·356 (0·032)	5·544 ± 2·408 (0·083)
Evergreen tree 1	*Arbutus menzesii*	13	0·704	0·075 ± 0·006 (< 0·001)	4·021 ± 0·785 (< 0·001)	0·682	6·137 ± 0·229 (< 0·001)	3·531 ± 0·727 (0·001)
	Umbellularia californica	12	0·203	0·126 ± 0·052 (0·035)	30·303 ± 18·998 (0·142)	0·079	4·892 ± 1·050 (0·001)	1·084 ± 1·168 (0·375)
Late successional (Bana) 3	*Aspidosperma album*	41	0·443	0·074 ± 0·008 (< 0·001)	5·340 ± 0·958 (< 0·001)	0·306	4·608 ± 0·192 (< 0·001)	2·752 ± 0·663 (< 0·001)
	Neea obovata	31	0·362	0·052 ± 0·004 (< 0·001)	4·457 ± 1·100 (< 0·001)	0·346	4·139 ± 0·517 (< 0·001)	2·962 ± 0·757 (0·001)
	Protium sp.	34	0·033	0·064 ± 0·004 (< 0·001)	2·685 ± 2·550 (0·300)	0·325	5·092 ± 0·333 (< 0·001)	2·991 ± 0·763 (< 0·001)
	Retiniphyllum truncatum	37	0·566	0·178 ± 0·020 (< 0·001)	13·246 ± 1·959 (< 0·001)	0·423	11·145 ± 1·196 (< 0·001)	12·005 ± 2·370 (< 0·001)
	Rhodognaphalopsis humilis	19	0·113	0·096 ± 0·038 (0·021)	5·772 ± 3·932 (0·160)	0·049	6·413 ± 0·846 (< 0·001)	2·611 ± 2·777 (0·360)
Late successional (Caatinga) 3	*Caraipa heterocarpa*	33	0·004	0·039 ± 0·016 (0·020)	0·823 ± 2·373 (0·731)	0·677	5·213 ± 0·327 (< 0·001)	5·221 ± 0·648 (< 0·001)
	Eperua leucantha	35	0·384	0·078 ± 0·006 (< 0·001)	7·488 ± 1·649 (< 0·001)	0·174	4·569 ± 0·327 (< 0·001)	2·510 ± 0·953 (0·013)
	Micrandra sprucei	34	0·551	0·083 ± 0·009 (< 0·001)	7·469 ± 1·192 (< 0·001)	0·697	4·019 ± 0·225 (< 0·001)	5·268 ± 0·614 (< 0·001)
	Micropholis maguirei	32	0·102	0·045 ± 0·014 (0·003)	2·783 ± 1·506 (0·075)	0·002	2·619 ± 0·257 (< 0·001)	0·182 ± 0·739 (0·807)
	Protium sp.	22	0·385	0·078 ± 0·015 (< 0·001)	7·033 ± 1·989 (0·002)	0·002	2·438 ± 0·753 (0·004)	0·338 ± 1·696 (0·844)

Table A1 continued.

			Mass based expression			Area based expression		
Community or vegetation type and citation number	Species	N	R^2	Centered intercept ± s.e. (P value) µmol g^{-1} s^{-1}	Slope ± s.e. (P value) µmol g^{-1} s^{-1}	R^2	Centered intercept ± s.e. (P value) µmol m^{-2} s^{-1}	Slope ± s.e. (P value) µmol g^{-1} s^{-1}
Late successional (Tierra Firme) 3	"Cabari" (Leguminaceae)	38	0·123	0·027 ± 0·009 (0·003)	2·996 ± 1·331 (0·031)	0·404	2·343 ± 0·405 (< 0·001)	2·382 ± 0·482 (< 0·001)
	Eperua purpurea	24	0·431	0·061 ± 0·003 (< 0·001)	4·027 ± 0·986 (< 0·001)	0·431	5·186 ± 0·546 (< 0·001)	4·802 ± 1·177 (0·001)
	Licania heteromorpha	35	0·196	0·070 ± 0·009 (< 0·001)	5·708 ± 2·011 (0·008)	0·695	4·733 ± 0·191 (< 0·001)	4·848 ± 0·558 (< 0·001)
	Ocotea costulata	29	0·055	0·055 ± 0·004 (< 0·001)	2·768 ± 2·216 (0·222)	0·285	4·275 ± 0·237 (< 0·001)	2·142 ± 0·653 (0·003)
	Protium sp.	22	0·084	0·057 ± 0·019 (0·007)	3·008 ± 2·217 (0·190)	0·196	5·242 ± 0·768 (< 0·001)	4·819 ± 2·184 (0·039)
Mid successional 3	*Goupia glabra*	21	0·348	0·086 ± 0·006 (< 0·001)	-7·419 ± 2·330 (0·005)	0·041	7·987 ± 0·416 (< 0·001)	1·395 ± 1·545 (0·378)
Old field annual 1	*Abutilon theophrasti*	4	0·477	0·103 ± 0·074 (0·297)	8·427 ± 6·242 (0·309)	0·437	9·529 ± 2·917 (0·082)	3·582 ± 2·874 (0·339)
	Ambrosia trifida	4	0·704	0·208 ± 0·041 (0·036)	6·825 ± 3·129 (0·161)	0·690	14·079 ± 2·712 (0·035)	8·691 ± 4·115 (0·169)
	Chenopodium album	5	0·668	0·170 ± 0·054 (0·052)	7·230 ± 2·944 (0·091)	0·871	12·069 ± 1·805 (0·007)	7·709 ± 1·713 (0·020)
	Polygonum pensylvanicum	8	0·114	0·220 ± 0·056 (0·008)	4·454 ± 5·066 (0·413)	0·522	12·896 ± 1·100 (< 0·001)	7·309 ± 2·857 (0·043)
Amazonian pioneer 3	*Solanum straminifolia*	6	0·467	-0·100 ± 0·253 (0·714)	21·124 ± 11·283 (0·134)	0·115	13·279 ± 2·285 (0·004)	5·728 ± 7·958 (0·512)
Pioneer (Tierra Firme) 3	*Cecropia ficifolia*	27	0·108	0·164 ± 0·025 (< 0·001)	6·144 ± 3·527 (0·094)	0·120	12·486 ± 1·466 (< 0·001)	5·770 ± 3·119 (0·076)
Secondary successional (Tierra Firme) 3	*Bellucia grossularioides*	18	0·817	0·115 ± 0·006 (< 0·001)	11·081 ± 1·311 (< 0·001)	0·354	9·139 ± 1·446 (< 0·001)	5·051 ± 1·707 (0·009)
	Clidemia sericea	18	0·803	0·125 ± 0·006 (< 0·001)	15·121 ± 1·875 (< 0·001)	0·740	9·551 ± 0·548 (< 0·001)	14·515 ± 2·150 (< 0·001)
	Miconia dispar	12	0·770	0·093 ± 0·006 (< 0·001)	7·070 ± 1·223 (< 0·001)	0·656	5·814 ± 0·796 (< 0·001)	8·856 ± 2·026 (0·001)
	Vismia japurensis	34	0·639	0·141 ± 0·007 (< 0·001)	14·239 ± 1·892 (< 0·001)	0·014	11·357 ± 0·879 (< 0·001)	1·584 ± 2·359 (0·507)
	Vismia lauriformis	22	0·846	0·132 ± 0·005 (< 0·001)	19·969 ± 1·905 (< 0·001)	0·609	9·288 ± 0·737 (< 0·001)	14·732 ± 2·638 (< 0·001)
Tropical cultivar 3	*Manihot esculenta*	14	0·451	-0·209 ± 0·163 (0·223)	24·860 ± 7·920 (0·009)	0·001	12·336 ± 2·455 (< 0·001)	0·720 ± 7·029 (0·920)

Table A2. Results for the mass and area-based regressions for individual species from the CO_2 experiments. Citations are: 1 = Norby *et al.* (1997); 2 = Vogel and Curtis (1995); 3 = Rey and Jarvis (1998); 4 = Forstreuter (1995); 5 = Gunderson and Wullschleger (1994); 6 = Curtis *et al.* (1995); 7 = Tissue *et al.* (in review); 8 = Whitehead *et al.* (1995); 9 = Tissue *et al.* (1997).

Tree type and citation number	Species	N	R^2	Centered intercept at ambient CO_2 ± s.e. (P value)	Slope at ambient CO_2 ± s.e. (P value)	Effect of elevated CO_2 on centered intercept ± s.e. (P value)	Effect of elevated CO_2 on slope ± s.e. (P value)	ANOVA P value
Mass based expression								
				μmol g^{-1} s^{-1}	μmol g^{-1} s^{-1}	μmol g^{-1} s^{-1}	μmol g^{-1} s^{-1}	
Deciduous 1	*Acer rubrum*	69	0·333	0·131 ± 0·018 (< 0·001)	8·796 ± 3·201 (0·008)	0·018 ± 0·022 (0·416)	10·190 ± 4·969 (0·044)	< 0·001
1	*Acer saccharum*	72	0·109	0·111 ± 0·007 (< 0·001)	1·252 ± 2·966 (0·674)	0·027 ± 0·012 (0·021)	7·047 ± 4·344 (0·109)	0·048
2	*Alnus glutinosa*	23	0·309	0·234 ± 0·091 (0·018)	7·740 ± 6·808 (0·270)	0·021 ± 0·137 (0·877)	10·593 ± 13·878 (0·455)	0·066
3	*Betula pendula*	45	0·370	0·153 ± 0·030 (< 0·001)	6·552 ± 3·920 (0·102)	0·048 ± 0·035 (0·178)	9·411 ± 5·504 (0·095)	< 0·001
4	*Fagus sylvatica*	87	0·468	0·098 ± 0·011 (< 0·001)	2·595 ± 1·793 (0·152)	0·065 ± 0·015 (< 0·001)	0·704 ± 2·668 (0·793)	< 0·001
5	*Liriodendron tulipifera*	23	0·516	0·120 ± 0·009 (< 0·001)	7·646 ± 3·792 (0·058)	0·051 ± 0·013 (0·001)	-5·786 ± 4·471 (0·211)	0·003
6	*Populus euramericana*	29	0·372	0·174 ± 0·033 (< 0·001)	5·835 ± 2·542 (0·030)	0·087 ± 0·041 (0·041)	-1·814 ± 3·259 (0·583)	0·008
Pine 7	*Pinus ponderosa*	27	0·642	0·084 ± 0·014 (< 0·001)	3·718 ± 2·380 (0·132)	0·081 ± 0·028 (0·008)	6·702 ± 4·127 (0·118)	< 0·001
8	*Pinus radiata*	33	0·352	0·105 ± 0·020 (< 0·001)	9·576 ± 8·765 (0·284)	0·019 ± 0·026 (0·471)	12·507 ± 10·255 (0·232)	0·005
9	*Pinus taeda*	42	0·442	0·099 ± 0·015 (< 0·001)	13·267 ± 3·329 (< 0·001)	0·073 ± 0·018 (< 0·001)	-6·310 ± 4·255 (0·146)	< 0·001
Area based expression								
				μmol m^{-2} s^{-1}	μmol g^{-1} s^{-1}	μmol m^{-2} s^{-1}	μmol g^{-1} s^{-1}	
Deciduous 1	*Acer rubrum*	69	0·201	8·724 ± 0·908 (< 0·001)	2·960 ± 2·458 (0·233)	6·221 ± 1·986 (0·003)	14·019 ± 5·199 (0·009)	0·002
1	*Acer saccharum*	72	0·215	6·810 ± 0·763 (< 0·001)	2·772 ± 1·694 (0·107)	2·725 ± 1·164 (0·022)	3·076 ± 2·460 (0·215)	0·001
2	*Alnus glutinosa*	23	0·683	20·715 ± 3·222 (< 0·001)	-1·830 ± 6·039 (0·765)	11·510 ± 5·182 (0·039)	0·969 ± 8·347 (0·909)	< 0·001
3	*Betula pendula*	45	0·299	11·253 ± 0·930 (< 0·001)	1·763 ± 2·699 (0·517)	4·223 ± 1·275 (0·002)	4·532 ± 3·506 (0·203)	0·002
4	*Fagus sylvatica*	87	0·787	6·971 ± 0·349 (< 0·001)	5·902 ± 0·779 (< 0·001)	5·332 ± 0·545 (< 0·001)	4·881 ± 1·159 (< 0·001)	< 0·001
5	*Liriodendron tulipifera*	23	0·684	8·249 ± 0·754 (< 0·001)	1·059 ± 2·600 (0·688)	5·684 ± 0·989 (< 0·001)	3·697 ± 3·033 (0·238)	< 0·001
6	*Populus euramericana*	29	0·574	14·787 ± 2·792 (< 0·001)	4·310 ± 2·985 (0·161)	14·277 ± 3·565 (< 0·001)	-5·778 ± 3·509 (0·112)	< 0·001
Pine 7	*Pinus ponderosa*	27	0·743	6·940 ± 0·630 (< 0·001)	4·234 ± 1·938 (0·039)	4·538 ± 0·967 (< 0·001)	3·183 ± 2·685 (0·248)	< 0·001
8	*Pinus radiata*	33	0·168	7·548 ± 0·564 (< 0·001)	4·140 ± 3·702 (0·273)	1·987 ± 0·854 (0·027)	-2·576 ± 4·070 (0·532)	0·142
9	*Pinus taeda*	42	0·528	7·314 ± 0·780 (< 0·001)	2·922 ± 1·672 (0·089)	3·862 ± 1·001 (< 0·001)	-0·117 ± 2·459 (0·962)	< 0·001