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Sensitivity of leaf photosynthesis to CO_2 concentration is an invariant function for C_3 plants: A test with experimental data and global applications

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Abstract. Rising atmospheric CO_2 concentration (C_a) may alter two components (sensitivity and acclimation) of global photosynthetic carbon influx into terrestrial ecosystems (P_G). Most existing global models focus on long-term acclimation. We have developed a leaf-level function ($\mathcal{L}$) to quantify short-term increment of P_G associated with sensitivity. The $\mathcal{L}$ function is the normalized response of leaf photosynthesis to a small change in C_a and has been suggested to be an invariant function for C_3 plants grown in diverse environments. This paper tests the hypothesis that $\mathcal{L}$ is an invariant function. We calculated values of $\mathcal{L}$ from 9 sets of experimental data which incorporated photosynthetic responses of 12 plant species to measurement conditions of light and temperature and to growth in different light, temperature, nitrogen, phosphorus, water stress, and CO_2 concentration. Absolute rates of leaf photosynthesis differed by more than tenfold due to species differences and environmental variation. However, $\mathcal{L}$ values derived from these data sets converged into a narrow range defined by two equations of the $\mathcal{L}$ function, confirming that $\mathcal{L}$ was insensitive to differences in photosynthetic capacity among species and between plants acclimated to different growth environments. Using the $\mathcal{L}$ function, we predict that a yearly increase of 1.5 parts per million (ppm) in C_a will induce an increase in P_G by 0.18 to 0.34 Gt (1 Gt = 10^{15} g) C yr^{-1} in 1993, provided that (1) P_G = 120 Gt C yr^{-1}, (2) 85% of P_G is generated by C_3 plant assimilation, and (3) the 1.5-ppm increase in C_a will not induce significant photosynthetic acclimation.

Introduction

An increase in atmospheric CO_2 concentration (C_a) considerably alters the global biogeochemical cycle of carbon in terrestrial ecosystems [*Melillo et al.*, 1990; *Schlesinger*, 1991]. Net primary production may be enhanced by increased CO_2 in a variety of ways including stimulation of photosynthesis [*Pearcy and Bjorkman*, 1983], depression of respiration [*Amthor et al.*, 1992], and possible alleviation of water or nutrient stresses [*Mooney et al.*, 1991]. Increased CO_2 concentration also potentially stimulates carbon allocation to soil compartments through increased root exudation [*Norby et al.*, 1987], accelerated root turnover rates [*Rogers et al.*, 1994], and greater litterfall [*Field et al.*, 1996]. Increased carbon availability in soil alters microbial populations and activities, affecting soil carbon release to the atmosphere [*Luo et al.*, 1996] and soil nutrient availability [*Johnson et al.*, 1996], which may strongly regulate photosynthetic carbon uptake and plant growth. Among all these processes, leaf photosynthesis has been identified as one of the primary processes which are directly responsive to the change in C_a [*Mooney et al.*, 1987].

Photosynthetic response to rising C_a has been studied on two general components: sensitivity [*Allen et al.*, 1987; *Kirschbaum*, 1994; *Luo and Mooney*, 1996; *Sharkey*, 1988; *Stitt*, 1991] and acclimation [*Curtis*, 1996; *Gunderson and Wullschleger*, 1994; *Luo et al.*, 1994; *Sage*, 1994; *Stitt*, 1991]. Acclimation may induce changes in photosynthetic capacity in plants grown at different CO_2 concentrations [*Luo et al.*, 1994; *Stitt*, 1991]. Photosynthetic capacity, for example, increased for plant species *Glycine max* [*Campbell et al.*, 1988] and decreased for *Gossypium hirsutum* [*Wong*, 1990] and *Lolium perenne* [*Ryle et al.*, 1992]. Photosynthetic acclimation may result from redistribution of nitrogen among various photosynthetic enzymes [*Sage et al.*, 1990], adjustments in source-sink relationships [*Stitt*, 1991], and balance between leaf biochemical composition and morphological structure [*Luo et al.*, 1994]. These acclimation changes are species-specific and vary with growth environment.

Sensitivity of leaf photosynthesis to CO_2 concentration is determined by competition between carboxylation and oxygenation of ribulose-bisphosphate (RuBP). Photosynthesis (i.e., carboxylation) and photorespiration (i.e., oxygenation) are both catalyzed by ribulose-1,5-bisphosphate carboxylase/oxygenase

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(rubisco) [*Andrews and Lorimer*, 1987]. Increased carbon dioxide concentration competes with oxygen and decreases the oxygenase activity of rubisco [*Farquhar et al.*, 1980; *Lawlor*, 1993], leading to an increased ratio of carboxylation to oxygenation. *Sharkey* [1988] demonstrated that the ratio of carboxylation to oxygenation declines, similarly among species, as C_a increases. *Stitt* [1991] estimated that photosynthesis will increase by 30 - 75% due to sensitivity when C_a is doubled from its present concentration. *Allen et al.* [1987] demonstrated that the relative response of photosynthesis to elevated CO_2 was similar among several agronomic species. *Kirschbaum* [1994] emphasized that sensitivity of photosynthetic response to C_a was temperature dependent and argued that responses of carbon influx from the atmosphere to ecosystems will differ in different temperature regions of the Earth. *Luo and Mooney* [1996] normalized leaf photosynthetic response to a small change in C_a (the normalized response was defined as a leaf-level $\mathcal{L}$ function) and suggested that the sensitivity (the $\mathcal{L}$ function) is independent of interspecific variation and growth environment, slightly affected by measurement light and temperature, and a function of C_a.

Mathematical analysis suggests that photosynthetic sensitivity is independent of acclimation [*Luo and Mooney*, 1995, 1996]. Acclimation may result in either an increase or a decrease in photosynthetic capacity and rate [*Gunderson and Wullschleger*, 1994; *Luo et al.*, 1994]. Sensitivity, however, always leads to an increase in photosynthetic rate as C_a is increased. Since the sensitivity is independent of acclimation, realized changes in leaf photosynthetic rate for plants grown at elevated CO_2 is the increment of carbon gain due to sensitivity plus or minus the acclimation change. If acclimation enhances photosynthesis, doubling C_a could lead to a greater than 70% increase in photosynthetic rate, the upper limit due to sensitivity. If acclimation reduces photosynthesis, then the increment in photosynthetic rate for a doubling of C_a may be less than 30%, the lower limit due to sensitivity.

Luo and Mooney [1995, 1996] proposed that the two concepts of photosynthetic sensitivity and acclimation can be applied to predict global photosynthetic carbon influx into terrestrial ecosystems (P_G, appendix). Since P_G is the sum of leaf photosynthesis, stimulation of P_G by an increase in C_a also has two components: sensitivity and acclimation. If a change in C_a is small enough such that photosynthetic acclimation is insignificant, then CO_2 stimulation of P_G is largely determined by sensitivity. Since sensitivity is an invariant function of CO_2 across different C_3 species and environmental conditions, *Luo and Mooney* [1996] proposed to estimate the additional amount of P_G (ΔP_G) stimulated by a yearly increase in C_a (ΔC_a) by multiplying $\mathcal{L}$ with P_G and ΔC_a (equation A5, appendix). If a change in C_a over the long term is large enough so that acclimation may considerably change photosynthetic capacity, then a change in global photosynthetic carbon influx is determined by both sensitivity and acclimation (equation A7, appendix). Long-term photosynthetic acclimation may be assessed by considering nitrogen-carbon interactions, vegetation redistribution, and growing season shift [*Luo and Mooney*, 1995; *Melillo et al.*, 1993; *Smith et al.*, 1992; *Potter et al.*, 1993; *VEMAP*, 1995].

The logic to link the leaf-level ($\mathcal{L}$) function directly with the CO_2 stimulation of P_G can be summarized in the following: First, since leaf photosynthesis is the primary pathway of carbon flow from the atmosphere to global terrestrial ecosystems, a change in P_G must result from changes in leaf photosynthesis. Second, direct extrapolation of leaf photosynthesis to predict P_G is generally not valid because of interspecific variation in photosynthetic properties and environmental heterogeneity. Thus, the challenge in scaling-up studies is how to reduce uncertainties associated with variation in environments and species characteristics. Third, photosynthetic changes in response to rising C_a have two components: sensitivity and acclimation. Acclimation varies with species and environments, whereas sensitivity is an invariant function of C_a. Acclimation has been found to be important when considering a large change in C_a, but for issues related to a small increase in C_a, such as yearly "missing carbon" and global terrestrial carbon sequestration, studying global-scale sensitivity of photosynthesis can be insightful. Fourth, since sensitivity is suggested to be independent of acclimation, ΔP_G estimated by using the $\mathcal{L}$ function should be valid for any reference P_G.

The $\mathcal{L}$ function has been applied to study the seasonal cycle of C_a (C.D. Keeling, J.F.S. Chin, and T.P. Whorf, Increased activity of northern vegetation inferred from atmospheric CO_2 measurements, submitted to *Nature*, 1996, hereafter referred to as C.D. Keeling et al. 1996), global terrestrial carbon sequestration (G.D. Farquhar, and J. Lloyd, Carbon sequestration associated with increasing levels of atmospheric CO_2, in preparation, 1996; Y. Luo, An integrated global terrestrial carbon sequestration model, submitted to *Global Biogeochemical Cycles*, 1996, hereafter refereed to as Y. Luo, 1996), and carbon and nitrogen interactions in terrestrial ecosystems [*Luo and Mooney*, 1995]. The $\mathcal{L}$ function quantifies the annual increment in P_G due to a small increase in C_a. It enables us to determine the percentage of the increase in the amplitude of the seasonal cycle of C_a at Mouna Loa, Hawaii and Point Borrow, Alaska that is due to the change in photosynthesis (C.D. Keeling et al., 1996). It also becomes possible to estimate nitrogen input that is required to balance the increased carbon uptake in terrestrial ecosystems on a yearly basis [*Luo and Mooney*, 1995]. Global terrestrial carbon sequestration results partly from differential increases in P_G and global respiration (R_G) associated with rising C_a (Y. Luo, 1996). Carbon, once fixed by photosynthesis, remains in terrestrial ecosystems for the duration of a global terrestrial carbon resident time (τ_G). For example, if τ_G is 5 years, this year's R_G is approximately equal to P_G 5 years ago. On the other hand, this year's P_G is equal to P_G of 5 years ago plus the increment caused by the increase in C_a over the past 5 years. The increment can be quantified by the $\mathcal{L}$ function.

The $\mathcal{L}$ function has the potential to become an important scaling parameter in studying global terrestrial carbon cycling in response to rising C_a. Although the concept of photosynthetic sensitivity embedded in the $\mathcal{L}$ function has been discussed in the literature [e.g., *Sharkey*, 1988], the invariance of sensitivity across various environmental variables and species characteristics has not been rigorously tested. The work presented in this paper is to determine whether the $\mathcal{L}$ function is an invariant function. In order to test this hypothesis, we used experimental data of photosynthesis (1) for plants acclimated to diverse growth environments of light, temperature, nitrogen, phosphorus, water stress, and CO_2 concentration; (2) for plants from a wide range of species with substantial differences in photosynthetic capacity; and (3) for plants exposed to different measurement conditions of light and temperature. In addition, the proposition that photosynthetic

sensitivity is independent of acclimation was tested. We also discuss the potential and limitations for using the $\mathcal{L}$ function to study global terrestrial carbon cycling.

Methods

Theory: Normalized Response of Photosynthesis to CO_2 Concentration (the Leaf-Level $\mathcal{L}$ Function)

The $\mathcal{L}$ function is simply derived from the *Farquhar et al.* [1980] model which describes leaf photosynthesis of C_3 plants as the minimum of

$$P_1 = J\frac{C_i - \Gamma}{4.5C_i + 10.5\Gamma} \quad \textbf{(1a)}$$

and

$$P_2 = V_{cmax}\frac{C_i - \Gamma}{C_i + K} \quad \textbf{(1b)}$$

where P_1 and P_2 are leaf gross photosynthesis limited by electron transport or rubisco activity, respectively, J is the electron transport rate (μmol electron m^{-2} s^{-1}), representing the effect of light on photosynthesis, V_{cmax} is the maximum carboxylation rate (μmol CO_2 m^{-2}, s^{-1}), which varies with leaf enzyme content and is regulated by both species characteristics and nutrient availability in ecosystems, C_i is the intercellular CO_2 concentration (parts per million (ppm)), Γ is the CO_2 compensation point without nonphotorespiratory respiration (ppm) and is related to temperature, and K is a coefficient (ppm) associated with enzyme kinetics ($= K_c(1+O/K_o)$, where K_c and K_o are Michaelis-Menton constants for CO_2 and oxygen, and O is oxygen concentration) and slightly varies with species. By varying these parameters, the *Farquhar et al.* [1980] model captures essential features of the environmental physiology of leaf photosynthesis.

Among all the parameters, J and V_{cmax} are most variable [*Wullschleger*, 1993]. V_{cmax} has been found to range from 6 μmol m^{-2} s^{-1} for *Picea abies*, to 194 μmol m^{-2} s^{-1} for *Beta vulgaris* [*Wullschleger*, 1993]. The parameter J increases with light in a rectangular-hyperbolic shape, eventually reaching a maximum (J_{max}) [*Farquhar et al.*, 1980]. The latter also greatly varies among species [*Wullschleger*, 1993]. High variability of these two parameters make it difficult to extrapolate leaf-level studies across scales of biological complexity.

In order to eliminate the parameters J and V_{cmax}, *Luo and Mooney* [1996] defined a leaf-level function ($\mathcal{L}$, ppm^{-1}) as

$$\mathcal{L} = \frac{1}{P}\frac{dP}{dC_i} \quad \textbf{(2)}$$

Mathematical derivation of (2) from (1) leads to two equations of this function as

$$\mathcal{L}_1 = \frac{15\Gamma}{(C_i - \Gamma)(4.5C_i + 10.5\Gamma)} \quad \textbf{(3a)}$$

and

$$\mathcal{L}_2 = \frac{K + \Gamma}{(C_i - \Gamma)(C_i + K)} \quad \textbf{(3b)}$$

Both parameters J and V_{cmax} are eliminated from equation (3) because $\mathcal{L}_1$ and $\mathcal{L}_2$ are a measure of normalized response. Eliminating J and V_{cmax} from the equation suggests that the $\mathcal{L}$ function is insensitive to light, nutrient availability, and species characteristics. The resultant $\mathcal{L}$ function varies with Γ, K, and C_i. Variation in the parameters Γ and K in response to the normal growth environment has been found to change predicted values of the $\mathcal{L}$ function by 15% or less [*Luo and Mooney*, 1996], suggesting that $\mathcal{L}$ is a function of only C_i.

Data Analysis

Validating the $\mathcal{L}$ function requires data of P/C_i (gross photosynthesis/intercellular CO_2 concentration) responses. We did not intend to exhaust all P/C_i response curves in the literature and rather used 1-2 data sets (1) for each measurement condition of light and temperature which greatly varied photosynthetic rates; (2) for a range of species with substantial differences in photosynthetic capacity; and (3) for each diverse growth environment of light, temperature, nitrogen, phosphorus, water stress, and CO_2 concentration which resulted in large differences in photosynthetic capacity. Data analyzed in this paper were either our own or from published P/C_i response curves in the literature.

Most P/C_i curves in the literature describe net rather than gross leaf photosynthesis as a function of C_i and, typically, leaf nonphotorespiratory respiration was either not measured or not reported. Although we realize that respiration rate is a complex function of many variables, there is an overall correlation between respiration rate and photosynthetic capacity [*Givnish*, 1988]. Lacking a more precise estimate, we used a mean respiration rate of 7.1% of photosynthetic rate [*Givnish*, 1988]. Estimated leaf respiration was added to net photosynthetic rate to obtain gross photosynthetic rate as a function of C_i in order to calculate $\mathcal{L}$ values. We also analyzed the sensitivity of the estimated $\mathcal{L}$ values to different values of leaf respiration using two methods. Theoretical analysis with equation (2) indicates that estimated $\mathcal{L}$ values changed by less than 10% when $C_i > 200$ ppm and up to 40% when $C_i < 200$ ppm when respiration rate ranged from 1.42 to 14.2% of photosynthetic rate. We also estimated $\mathcal{L}$ values using three respiration rates, that is, 1.42, 7.1, and 14.2% of photosynthesis, for each set of data used in this study. Sensitivity is expressed as the deviation between experimental and predicted $\mathcal{L}$ values.

Experimental data of gross photosynthesis in response to intercellular CO_2 concentration (C_i) were converted to $\mathcal{L}$ values by a difference equation as

$$\mathcal{L} = \frac{1}{(P_j + P_{j-1})/2}\frac{P_j - P_{j-1}}{C_{i,j} - C_{i,j-1}} \qquad j = 2, 3, \ldots n \quad \textbf{(4)}$$

where subscript j denotes the sequential number of observed data in one P/C_i response curve.

Traditional statistical methods are not readily applicable for analyzing consistency between theoretical predictions and experimental data of the $\mathcal{L}$ values. First, there are two theoretical curves for the $\mathcal{L}$ function, representing photosynthesis limited by RuBP regeneration and rubisco, respectively. Experimental data are expected to oscillate between the two curves, depending on environmental conditions. No conventional statistical methods are

available to analyze fitness of one data set with two theoretical curves. Second, the value of parameters Γ and K in equation (3) have been determined biochemically and vary with measurement temperature [*Brooks and Farquhar*, 1985; *Harley et al.*, 1992; *Jordan and Ogren*, 1984]. Neither K nor Γ could be freely determined with traditional regression methods.

In this study, we calculated the deviation of experimental data from the predicted range of $\mathcal{L}$ values (data points within the range treated as zero deviation) and the deviation of experimental data from their mean. Then, the sums of squares of the two deviations were calculated and used to compute a ratio. We used this ratio to represent the portion of variation in the experimental $\mathcal{L}$ values which can be explained by the theoretical curves of the $\mathcal{L}$ function (equivalent to conventional determinant coefficient, r^2). We exclude $\mathcal{L}$ values when $C_i < 189$ ppm (=0.7 × 270; the former is a common value of C_i/C_a (intercellular/atmospheric CO_2 concentrations) ratio and the latter is a preindustrial level of atmospheric CO_2 concentration) for computing r^2. In addition, we used a t test for paired comparisons to describe the probability that experimental data are significantly different from (either above or below) the predicted range of the $\mathcal{L}$ function. Predicted $\mathcal{L}$ values corresponding to each experimental $\mathcal{L}$ value was calculated with a given C_i. Both predicted and experimental $\mathcal{L}$ values were logarithmically transformed before the differences between them were used to compute t values and probability. We developed our own computer program for the above calculations. Theoretical values of the $\mathcal{L}$ function were calculated with different Γ and K corresponding to measurement temperature in each experiment.

An Uncertainty Index

Mathematical derivation of the $\mathcal{L}$ function eliminates parameters J and V_{cmax} and then reduces variation in P/C_i responses associated with environmental conditions and species characteristics. Experimental data, however, are still expected to vary between the two curves (equation (3a) and (3b)) defined by photosynthesis limited by either RuBP regeneration or rubisco. In addition, parameters Γ and K vary with measurement temperature, also leading to variation in $\mathcal{L}$ values. In order to assess the uncertainty of the $\mathcal{L}$ function, we defined an uncertainty index (UCI) as

$$UCI = \frac{\mathcal{L}_2 - \mathcal{L}_1}{\overline{\mathcal{L}}} \quad (5)$$

and

$$\overline{\mathcal{L}} = \frac{\mathcal{L}_1 + \mathcal{L}_2}{2} \quad (6)$$

Equation (5) describes theoretical values of uncertainty associated with the $\mathcal{L}$ function. We also calculated UCI with experimental data by substituting $\mathcal{L}_2$ in equation (5) with experimental $\mathcal{L}$ values calculated from the P/C_i responses.

Results

The $\mathcal{L}$ Function and Measurement Conditions of Light and Temperature

Photosynthetic rates of plant species *Phaseolus vulgaris* varied widely with measurement photon flux density (PFD), differing about sixfold between 100 and 1050 μmol m^{-2} s^{-1} (Figure 1a). The $\mathcal{L}$ values derived from this data set with equation (4) were, however, converged into a narrow range as defined by equations (3a) and (3b) (Figure 1b). Statistically, 91% of the variation in experimental $\mathcal{L}$ values was explained by the theoretical $\mathcal{L}$ function (Table 1). Thus we greatly reduced the variability of the P/C_i responses associated with short-term light fluctuation by using the $\mathcal{L}$ function. The paired comparison t test showed that experimental data were not significantly different from the predicted range of the $\mathcal{L}$ function when respiration was assumed to be 1.42 or 7.1% of the photosynthetic rate ($p = 0.586$ and 0.078, respectively, Table 1). However, when respiration was 14.2% of the photosynthetic rate, data were significantly different from predictions ($p = 0.003$, Table 1). We also calculated $\mathcal{L}$ values for species *Chenopodium album* with measurement PFD varying from 100 to 1050 μmol m^{-2} s^{-1} (data from *Sage et al.* [1990]). Derived $\mathcal{L}$ values fall in the same narrow range as depicted in Figure 1b (data not presented here).

On a finer scale, $\mathcal{L}$ values calculated from measurements made under high light conditions fall near the upper (rubisco-limited) line and those under low light conditions fall near the lower (RuBP regeneration-limited) line (Figure 1b). This result was consistent with predictions from equations (3a) and (3b). Under high light, rubisco limits photosynthesis and the normalized photosynthetic response is determined by the rubisco-catalyzed carboxylation rate, while under low light, RuBP regeneration limits photosynthesis. In general, rubisco-catalyzed carboxylation is more sensitive to changes in CO_2 concentration than RuBP regeneration.

Variation in the measurement temperature from 18° to 32°C yielded a substantial difference in the photosynthetic rate of *Eucalyptus pauciflora* (Figure 1c). However, $\mathcal{L}$ values derived from these data also fall close to the same narrow range found in Figure 1b (Figure 1d), suggesting that the $\mathcal{L}$ function is robust under short term variation in light and temperature. On a finer scale, $\mathcal{L}$ values from measurements conducted at high temperatures were closer to the upper limit, whereas $\mathcal{L}$ values from measurements made at low temperatures were closer to the lower limit (Fig 1d). A decrease in measurement temperature reduced the CO_2 compensation point (Γ) and enzyme kinetics (K), reducing $\mathcal{L}$ values, and an increase in measurement temperature increased $\mathcal{L}$ values (see equation (3)). When a temperature of 18°C was used to define a new lower limit (the lower dashed line) and 32°C to define a new upper limit (the upper dashed line), the new range envelopes most of the $\mathcal{L}$ values derived from the measurement data. About 89% of the variation in experimental $\mathcal{L}$ values was explained by the theoretical $\mathcal{L}$ function with the new predicted range (Table 1). The t test indicated that experimental data was consistent with the predicted $\mathcal{L}$ function when respiration was either 1.42, 7.1, or 14.2% of the leaf photosynthesis (Table 1).

The $\mathcal{L}$ Function and Growth Environments of Light, Temperature, Nitrogen, Phosphorus, Water Stress, and CO_2 Concentration

When plant species *Alocasia macrorrhiza* were grown in a range of light levels, leaf acclimation resulted in a wide variation in photosynthetic capacity, high for plants grown in high light and low for plants grown in low light. Consequently, photosynthetic rates measured at light saturation also varied greatly at a given C_i

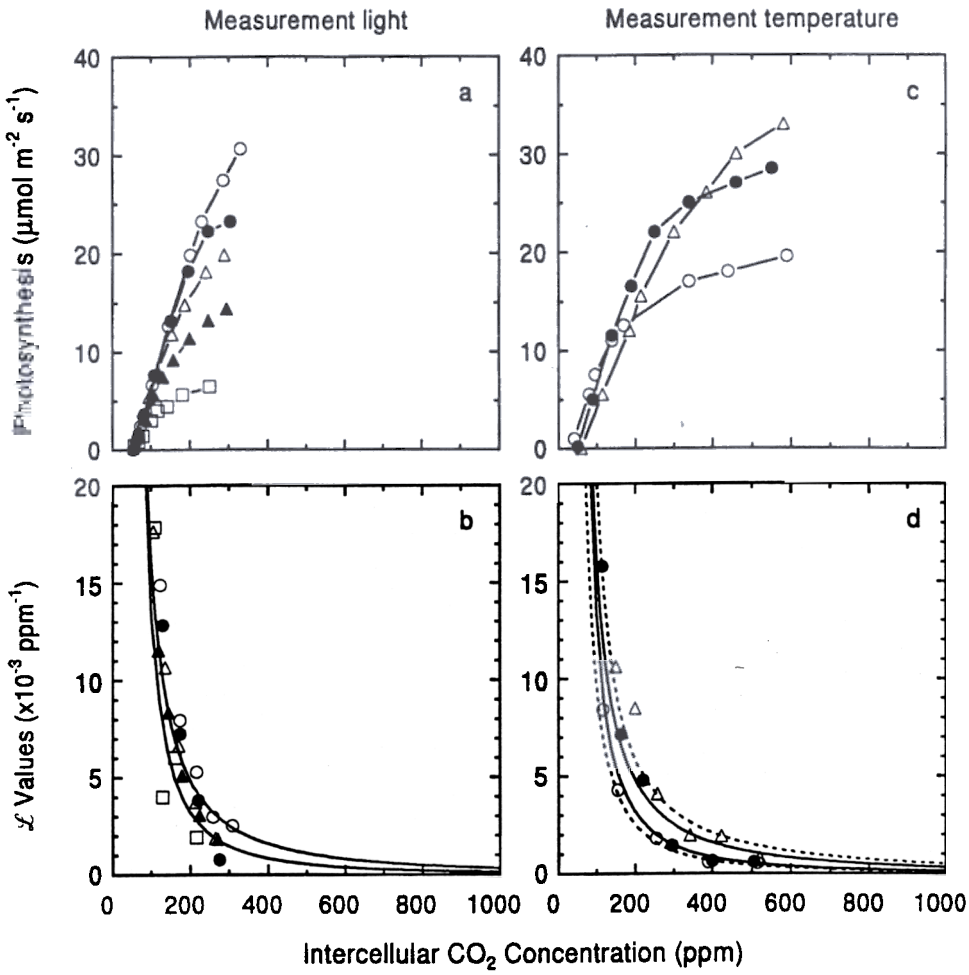

Figure 1. Effects of measurement photon flux density (PFD) and temperature on the photosynthetic responses to intercellular CO_2 concentration (C_i) and the $\mathcal{L}$ function (normalized response of photosynthesis to C_i changes). (a) Photosynthetic rates of plant species *Phaseolus vulgaris* measured at a PFD of 100 (open squares), 200 (solid triangles), 320 (open triangles), 500 (solid circles), and 1050 μmol m^{-2} d^{-1} (open circles) (data from *Sage et al.* [1990]). Plants were grown at PFD of 35 mol m^{-2} d^{-1}. (b) Values of the $\mathcal{L}$ function derived from the data set in Figure 1a according to equation (4) (represented by the same symbols as in Figure 1a). Solid lines are the predicted $\mathcal{L}$ function by equations (3a) and (3b) with Γ = 45 ppm and K = 414 ppm at 25°C (parameter values of Γ and K are defined according to [*Harley et al.*, 1992]). Lower line is $\mathcal{L}_1$ (light limitation) and upper line is $\mathcal{L}_2$ (rubisco limitation). (c) Photosynthetic rates of *Eucalyptus pauciflora* measured at 18 (open circles), 25 (solid circles), and 32°C (open triangles) (data from *Kirschbaum and Farquhar* [1984]). (d) Values of the $\mathcal{L}$ function derived from the same data set and represented by the same symbols as in Figure 1C. Solid lines are the same $\mathcal{L}$ function as in Figure 1b with Γ = 45 ppm and K = 414 ppm at 25°C. The upper dashed line is the predicted $\mathcal{L}_2$ function with Γ = 55 ppm and K = 835 ppm for a temperature of 32°C and the lower dashed line is $\mathcal{L}_1$ with Γ = 25 ppm and K = 200 ppm at 18°C.

(Figure 2a). But $\mathcal{L}$ values derived from the same data set closely corresponded to the narrow range found in Figure 1b and 1d (Figure 2b). Statistically, about 92% of the variation in experimental $\mathcal{L}$ values was explained by the theoretical $\mathcal{L}$ function and experimental data were not significantly different from the predicted range for all three respiration rates (Table 1). Photosynthesis, when measured at light saturation, is predicted to be limited by rubisco at low C_i and limited by RuBP regeneration at high C_i. Derived $\mathcal{L}$ values were scattered around the upper limit of the $\mathcal{L}$ function, which is defined by rubisco-limited photosynthesis, when C_i was less than approximately 350 ppm. The $\mathcal{L}$ values were scattered around the lower limit, which is defined by RuBP regeneration-limited photosynthesis, for C_i above approximately 450 ppm.

Growth of plants from 4 species at two temperatures, three nitrogen levels, three phosphorus levels, four water stress levels, and two CO_2 concentrations resulted in substantial differences in photosynthetic capacity and photosynthetic rates at a given C_i (Figures 2c, 3a, 3c, 4a, and 4c, respectively) but not in $\mathcal{L}$ (Figures 2d, 3b, 3d, 4b, and 4d, respectively), suggesting that the $\mathcal{L}$ function was independent of variation in these growth environments. Approximately 87-93% of the variation in

Table 1. Statistical Analysis on the Fitness of the $\mathcal{L}$ Function With Experimental Data

Treatment	Plant Species	r^2	p Values, Respiration 1.42%	7.1%	14.2%	N
		Measurement Conditions				
Light	*Phaseolus vulgaris*	0.91	0.586	0.078	0.003	40
Temperature	*Eucalyptus pauciflora*	0.89	0.732	0.787	0.223	21
		Growth Environments				
Light	*Alocasia macrorrhiza*	0.92	0.774	0.613	0.096	43
Temperature	*Pinus ponderosa*	0.87	0.523	0.324	0.101	63
Nitrogen	*Triticum aestivum*	0.90	0.043	0.043	0.013	19
Phosphorus	*Triticum aestivum*	0.88	0.074	0.095	0.017	14
Water stress	*Encelia frutescens*	0.93	0.031	0.085	0.003	23
CO_2 concentration	*Brassica oleracea*	0.86	0.798	0.809	0.414	17
		Interspecific Variation				
Species	7 species	0.90	0.033	0.038	0.002	50
		Pooled Data From All the Above Data Sets				
All treatments		0.89	0.004	0.043	0.001	286

Quantitative measures of the variation in the experimental $\mathcal{L}$ values that can be explained by theoretical prediction of the $\mathcal{L}$ function (equivalent to determinant coefficient, r^2); $\mathcal{L}$ values at C_i < 189 ppm were excluded for analysis, see text for explanation) and the probability (p value) that experimental $\mathcal{L}$ values are significantly different from (either above or below) the predicted range of the $\mathcal{L}$ function when estimated nonphotorespiratory respiration is either 1.42, 7.1, or 14.2% of leaf photosynthetic rate. N denotes the sample size.

experimental $\mathcal{L}$ values was explained by the theoretical $\mathcal{L}$ function for plants acclimated to these growth environments (Table 1). Experimental data were not significantly different from the theoretical prediction for *Pinus ponderosa* grown at two temperatures and *Brassica oleracea* grown at two CO_2 concentrations (Table 1). Experimental data were significantly different from the predicted range for *Triticum aestivum* grown at three nitrogen concentrations for all three respiration rates, but not for *Encelia frutescens* grown at four water stress levels and *T. aestivum* grown at three phosphate levels when respiration rates were 7.1% of leaf photosynthesis (Table 1).

The $\mathcal{L}$ Function and a Range of Species

A comparison of 7 species (plus other 5 species in Figures 1-4) indicates considerable variation in photosynthetic capacity and rates at a given C_i (Figure 5a) but no difference in $\mathcal{L}$ values (Figure 5b), suggesting that the $\mathcal{L}$ function is an invariant function for C_3 species. The $\mathcal{L}$ values were scattered around the upper limit when C_i was low and the lower limit when C_i was high. 90% of the variation in experimental $\mathcal{L}$ values pooled from the seven species was explained by the single theoretical $\mathcal{L}$ function. Experimental data were significantly different from the predicted range of the $\mathcal{L}$ function (Table 1).

The $\mathcal{L}$ Function and Pooled Data From All of the nine Data Sets

The 286 experimental data points pooled from the 12 species exposed to 8 environmental variables were closely scattered along the narrow range defined by the two equations, (3a) and (3b), of the $\mathcal{L}$ function with Γ = 45 ppm and K = 414 ppm at 25°C (Figure 6). Statistical analysis indicated that 89% of variation in the 185 data points (101 data points whose C_i < 189 ppm were excluded for regression analysis) was explained by the theoretical range of the $\mathcal{L}$ function (Table 1). We also calculated the deviation of experimental data from a mean of $\mathcal{L}_1$ and $\mathcal{L}_2$ instead of the predicted $\mathcal{L}$ range to include variation within the range, the resultant r^2 is lowered by 0.16, being 0.73. That means 73% of variation in the 185 data points was explained by the mean of two curves of the $\mathcal{L}$ function. In other words, setting data points within the theoretical range of the $\mathcal{L}$ function to be zero deviation substantially increases the r^2 value. In addition, the pooled data were significantly different from the predicted range with probability values being 0.004, 0.043, and 0.001 when respiration rates were 1.42, 7.1, and 14.2%, respectively, of leaf photosynthesis (Table 1).

Uncertainties of the $\mathcal{L}$ Function

Relative to mean values of the $\mathcal{L}$ function ($(\mathcal{L}_1 + \mathcal{L}_2)/2$), theoretical values of *UCI* (the solid line) vary from -0.14 at C_i = 0 ppm to 0.41 at C_i = 1000 ppm when measurement temperature is 25°C (Figure 7). At a current operational level of C_i ranging from 220 to 270 ppm, *UCI* is about 0.3, suggesting that shifting between $\mathcal{L}_1$ and $\mathcal{L}_2$ can cause a 30% difference in the $\mathcal{L}$ function. Variation in measurement temperature from 18° to 28°C will lead to a less than 20% change in *UCI*. *UCI* greatly increases when measurement temperature exceeds 35°C. At high C_i (e.g., >400 ppm) photosynthesis is almost always limited by RuBP regeneration, even when light levels are high. As a result, experimental values of $\mathcal{L}$ are expected to be scattered only around $\mathcal{L}_1$ which is defined by the RuBP regeneration-limited

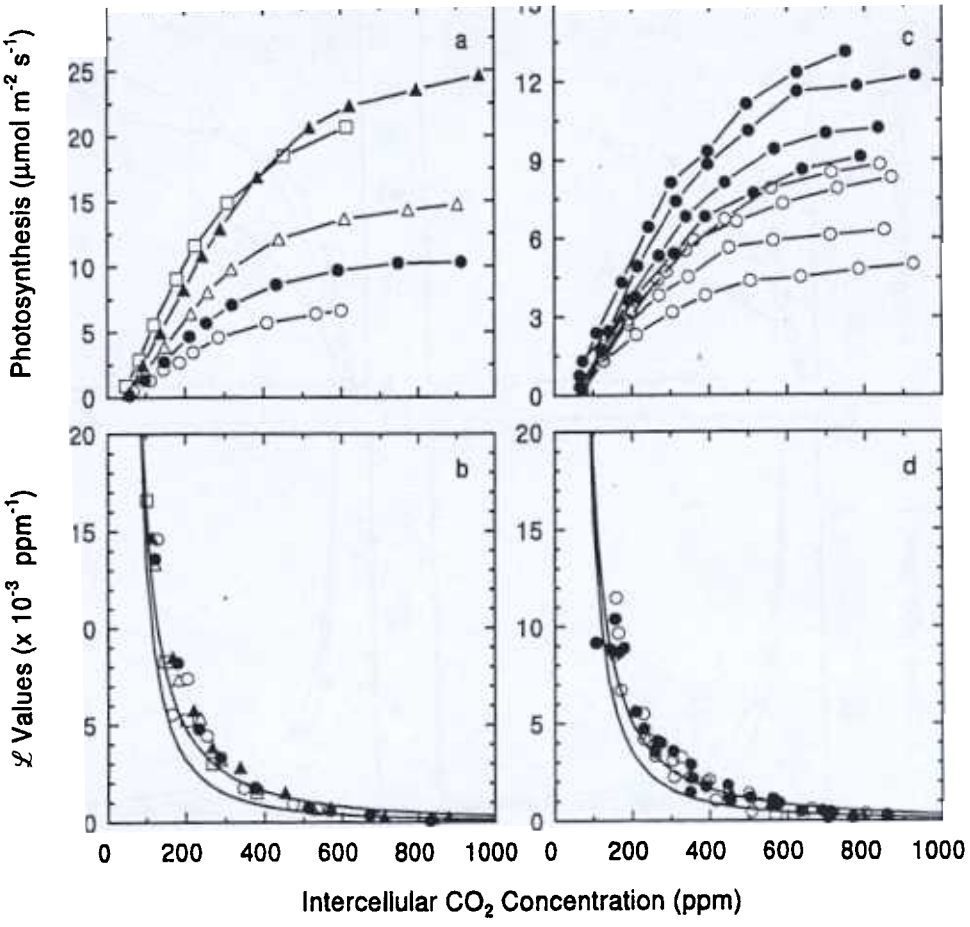

Figure 2. Effects of growth PFD and temperature on the photosynthetic responses to intercellular CO_2 concentration and the $\mathcal{L}$ function (normalized response of photosynthesis to C_i changes). Photosynthetic rates (a) and derived $\mathcal{L}$ values (b) of *Alocasia macrorrhiza* grown at a PFD of 0.79 (open circles), 1.7 (solid circles), 6.6 (open triangles), 14.8 (solid triangles), and 23.9 mol m^{-2} d^{-1} (open squares) and measured at saturating PFD (data from *Sims and Pearcy* [1989]). Photosynthetic rates (c) and derived $\mathcal{L}$ values (d) of *Pinus ponderosa* grown at control temperature (solid circles), control temperature + 5°C (open circles) for 160 days (data from R.B. Thomas, D.T. Tissue, J.D. Lewis, Duke University, unpublished, 1995). Four plants were measured for each temperature treatments. The control temperature is the mean at Placerville, California, the natural habitat of this species, adjusted every week to follow seasonal change, that is, day/night at planting was 17°/9°C (March 31, 1994), peaked in late July/early August at 28°/23°C, continued to decrease slowly until the end of experiment in October at 22°/15°C. Measurement was made at the growth temperature. Solid lines in Figure 2b and 2d are the same predicted $\mathcal{L}$ function as in Figure 1b.

photosynthesis. Thus, actual *UCI* of the $\mathcal{L}$ function will be lower than theoretical *UCI* when C_i is high.

Experimental values of *UCI* are scattered from -1 to 2.6 (Figure 7). Large variation in *UCI* in the low range of C_i is partly due to high sensitivity of $\mathcal{L}$ values to measurement errors of photosynthesis. *UCI* in the high range of C_i, on average, approaches zero, consistent with the mechanism that photosynthesis is limited only by RuBP regeneration at high C_i. The two outliers at C_i of about 600 ppm were associated with the two deviants in the A/C_i response curves of *Brassica oleracea* in elevated CO_2 (Figure 4c), possibly resulting from measurement errors. *UCI* within the C_i range of 200 to 400 ppm is expected to be relatively high because of interspecific variation in rubisco or RuBP regeneration which limits photosynthesis. The experimental values of *UCI* was described by a linear regression line $UCI = 0.412 - 0.00054\ C_i$ (the dotted line; $r^2 = 0.052$, $p = 0.0003$, where r^2 is determinant coefficient, and p is a value of probability).

Discussion

Experimental data support the hypothesis that the normalized photosynthetic response to CO_2 concentration (the $\mathcal{L}$ function) is insensitive to variations in photosynthetic capacity among species and between plants acclimated to different growth environments

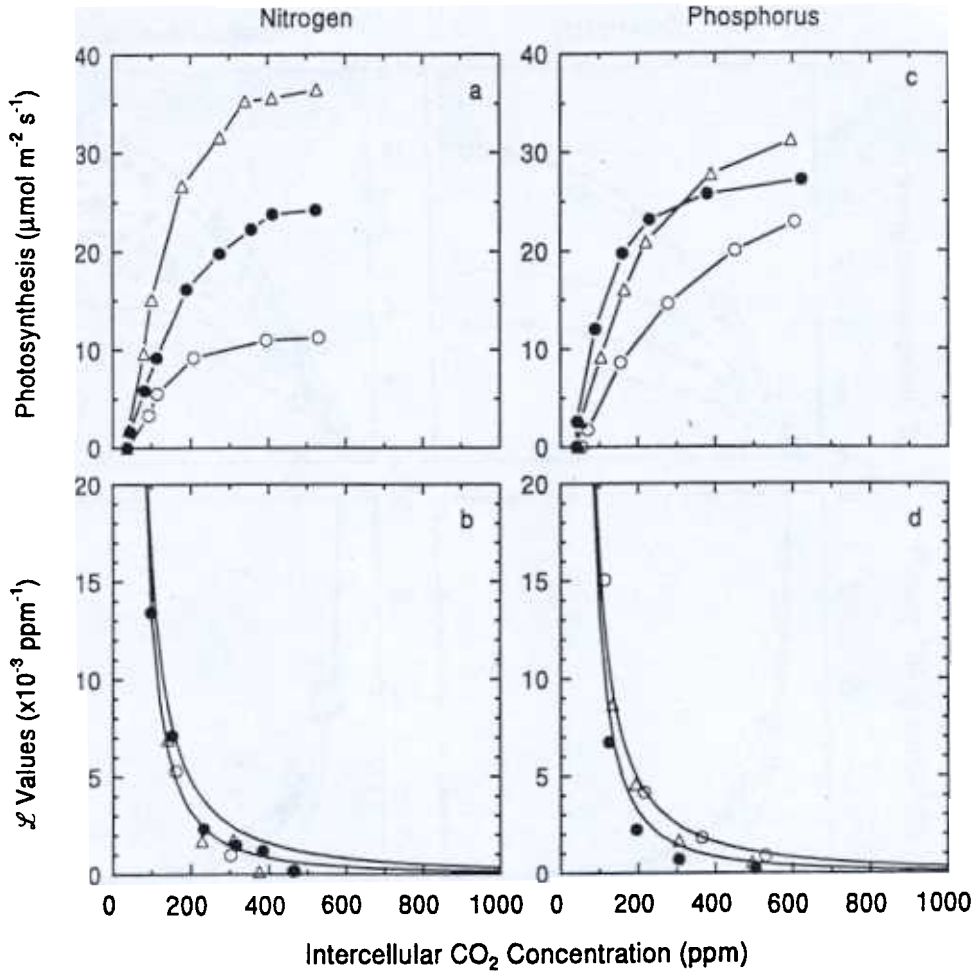

Figure 3. Effects of nitrogen and phosphorus on the photosynthetic responses to intercellular CO_2 concentration and the $\mathcal{L}$ function (normalized response of photosynthesis to C_i changes). Photosynthetic rates (a) and derived $\mathcal{L}$ values (b) of *Triticum aestivum* grown with 12 (open triangles), 2 (solid circles) and 0.1 m*M* NO_3^{-1} (open circles), measured at 1800 μmol quanta m^{-2} s^{-1}, and 23°C. (data from *Evans* [1985]). Photosynthetic rates (c) and derived $\mathcal{L}$ values (d) of *Triticum aestivum* grown at 0 (open circles), 0.5 (solid circles), and 10 (open triangles) mol m^{-3} phosphate concentration (data from *Jacob and Lawlor* [1991]). Plants were grown with 350 - 400 μmol quanta m^{-2} s^{-1} photosynthetic active radiation (PAR) for 16 h, 22°/20°C day/night temperature. Solid lines in Figure 3b and 3d are the same predicted $\mathcal{L}$ function as in Figure 1b with Γ = 42 ppm and K = 337 ppm at 23°C.

of light, temperature, nitrogen, phosphorus, water stress, and CO_2 concentration. Indeed, the theoretical range of the $\mathcal{L}$ function can explain 89% of the variation in 185 experimental $\mathcal{L}$ values with corresponding C_i > 189 ppm, pooled from the 12 species in the six growth environments and the two measurement conditions. Difference in the relative control of RuBP regeneration and rubisco on photosynthesis and the dependence of photosynthesis on measurement temperature may cause a 30% uncertainty in the $\mathcal{L}$ function at current C_a (Figure 7).

The *t* tests for paired comparisons indicate that 2 out of 9 sets of data examined in this study were significantly different (p < 0.05) from the predicted range of the $\mathcal{L}$ function when nonphotorespiratory respiration was 7.1% of leaf photosynthetic rate. Difference between experimental data and predictions of the $\mathcal{L}$ function may result from several causes, including data errors and physiological processes which have not yet been incorporated into the $\mathcal{L}$ function. Estimation of leaf respiration according to photosynthetic rate is physiologically based [*Givnish*, 1988] but not actual values of respiration. If actual respiration is larger than the estimated one, experimental $\mathcal{L}$ values will be smaller than those plotted in Figures 1-6, resulting in experimental data that occur above the predicted range and vice versa. Physiological processes that may cause the discrepancy include inorganic phosphate limitation of photosynthesis and patchy stomatal opening. The data set on *Triticum aestivum* which we used to represent phosphorus treatments (Figure 3c and 3d) indicated that de-sensitization of photosynthetic response to a CO_2 increase occurred with 0.5 mol m^{-3} but not with 0 and 10 mol m^{-3} phosphate concentrations [*Jacob and Lawlor*, 1991]. We also analyzed the data set on *Pinus taeda* with the limiting supply of phosphorus [*Lewis et al.*, 1994]. The $\mathcal{L}$ values derived from that data set are consistent with prediction of the $\mathcal{L}$ function when C_i

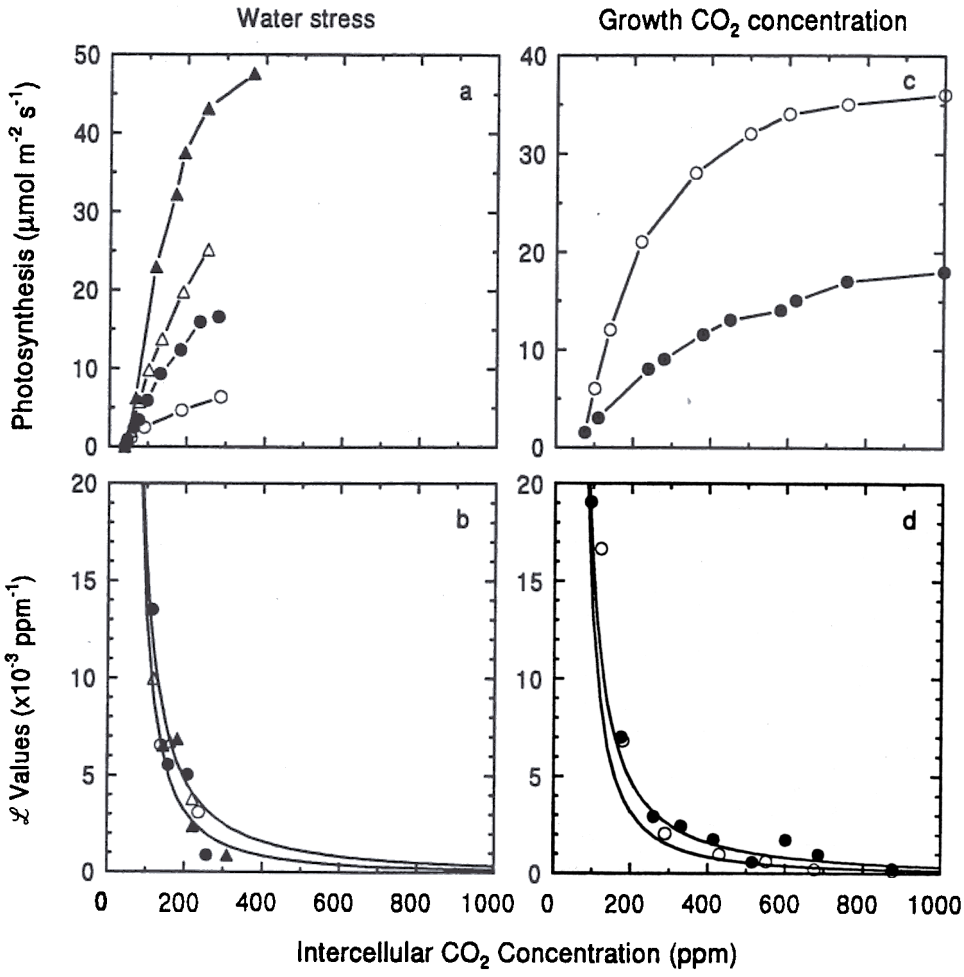

Figure 4. Effects of water stress and growth CO_2 concentration on the photosynthetic responses to intercellular CO_2 concentration and the $\mathcal{L}$ function (normalized response of photosynthesis to C_i changes). Photosynthetic rates (a) and derived $\mathcal{L}$ values (b) of *Encelia frutescens* at a leaf water potential of -1.9 MPa (solid triangles), -3.2 MPa (open triangles), -3.6 MPa (solid circles), and -4.0 MPa (open circles) (data from *Comstock and Ehleringer* [1984]). Plants were grown at daily PAR of 40-50 mol m^{-2} and daily temperature ranges from 25° to 35°C. Photosynthesis was measured at 1.8 mmol photon m^{-2} s^{-1} and 30°C. Solid lines in Figure 4b are the same predicted $\mathcal{L}$ function with Γ = 50 ppm and K = 686 ppm at 30°C. Photosynthetic rates (a) and derived $\mathcal{L}$ values (b) of *Brassica oleracea* grown at a CO_2 concentration of 340 ppm (open circles) and 680 ppm (solid circles) (data from *Sage et al.* [1989]). Plants were grown at PFD of 35 mol m^{-2} d^{-1} and photosynthesis was measured at 25°C. Solid lines in Figure 4d are the same predicted $\mathcal{L}$ function as in Figure 1b.

is below 400 ppm and are negative at C_i = 480 and 700 ppm. Theoretical analysis indicates that phosphate limitation not only desensitizes CO_2 stimulation [*Sharkey*, 1985] but also possibly reduces photosynthesis [*Harley and Sharkey*, 1991] as CO_2 concentration increases, leading to negative $\mathcal{L}$ values. That response cannot be predicted by equations (3a) and (3b). Stomatal patchiness may develop as CO_2 concentration increases during measurement of P/C_i responses, especially in the stressed conditions (Z. Cardon, personal communication, 1995). We have not found suitable data sets to test effects of stomatal patchiness on the $\mathcal{L}$ function.

Photosynthetic sensitivity is apparently independent of acclimation (Figure 4c and 4d). Photosynthetic acclimation to various growth CO_2 concentrations leads to adjustments in leaf properties, resulting in a substantial difference in photosynthetic capacity and rates (Figure 4c; also see [*Luo et al.*, 1994]). Acclimation, however, does not change the sensitivity of photosynthetic response to CO_2 concentration (Figure 4d). The latter is determined by competition between carboxylation and oxygenation of RuBP [*Andrews and Lorimer*, 1987]. Thus, the $\mathcal{L}$ function which is the measure of sensitivity is independent of acclimation.

The $\mathcal{L}$ function can be directly linked to atmospheric CO_2 concentration (C_a) using an equation $C_i = \alpha\, C_a$, where α is a coefficient of proportionality of C_i against C_a [*Luo and Mooney*, 1996]. Thus, equations (3a) and (3b) become

$$\mathcal{L}_1 = \frac{15\,\alpha\,\Gamma}{(\alpha\, C_a - \Gamma)(4.5\,\alpha\, C_a + 10.5\,\Gamma)} \qquad \textbf{(7a)}$$

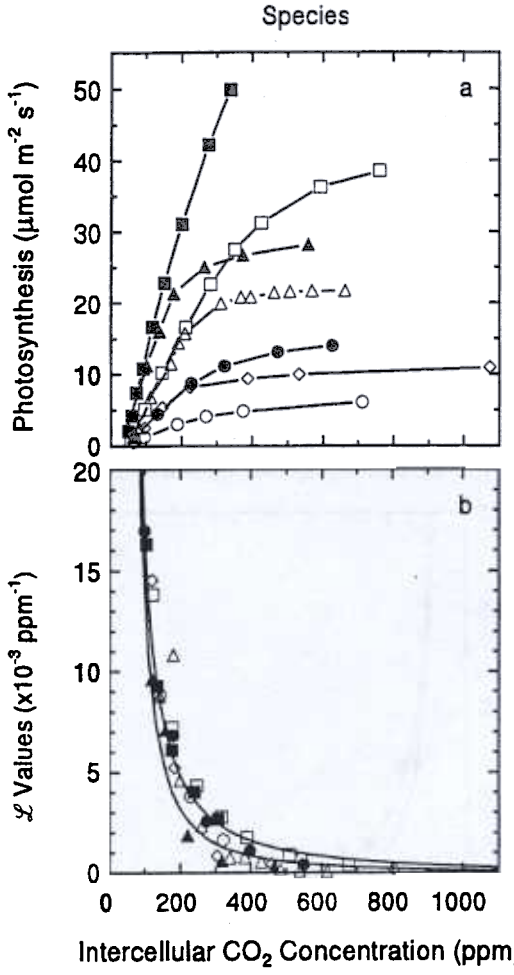

Figure 5. Interspecific variation of the photosynthetic responses to intercellular CO_2 concentration and the $\mathcal{L}$ function (normalized response of photosynthesis to C_i changes). Photosynthetic rates (a) and derived $\mathcal{L}$ values (b) of *Castanea sativa* (solid circles, data from *Goddard* [1989]), *Chenopodium album* (solid squares, data from *Sage et al.* [1990]), *Colocasia esculenta* (open squares, data from *Sims and Pearcy* [1989]), *Picea engelmannii* (open circles, data from *Delucia* [1986]), *Pinus ponderosa* (open diamonds, data from J.T. Ball, Desert Research Institute, unpublished, 1995), *Senecio vulgaris* (open triangles, data from *Ireland et al.* [1988]), *Triticum aestivum* (solid triangles, data from *Azcon-Bieto* [1983]). Solid lines in Figure 5b are the predicted $\mathcal{L}$ function as in Figure 1b with Γ = 45 ppm and K = 414 ppm at 25°C.

$$\mathcal{L}_2 = \frac{\alpha(K+\Gamma)}{(\alpha C_a - \Gamma)(\alpha C_a + K)} \qquad (7b)$$

Wong et al. [1985a, b, and c] have demonstrated with species *Eucalyptus pauciflora, Gossypium hirsutum, Phaseolus vulgaris,* and *Zea mays* that the C_i/C_a ratio (α) remains almost constant for plants grown at different levels of nitrogen, phosphorus, light intensity, water stress, photoinhibition, and ambient partial pressure of CO_2 and with different measurement light intensity. They also surveyed the additional five C_3 species, leading to a conclusion that α is nearly constant for C_3 plants. Other studies [*Beerling and Woodward,* 1995; *Polley et al.,* 1993] also indicate that α is nearly constant for a wide variety of species. With a constant α, the $\mathcal{L}$ function predicted by equations (7a) and (7b) should be α times that predicted by equations (3a) and (3b). In the case that α varies with species and growth environment by 10%, the predicted $\mathcal{L}$ values should change less than 10% [*Luo and Mooney,* 1996]. Comparison of experimental $\mathcal{L}$ values calculated from P/C_a (photosynthesis/ambient CO_2) curves with these from P/C_i curves suggested that variation in C_i/C_a from 0.65 to 0.85 does not significantly affect the $\mathcal{L}$ function (K.L. Griffin and Y. Luo, Sensitivity of *Glycine max* L. leaf photosynthesis and stomata to CO_2 partial pressure, A direct test of the $\mathcal{L}$ function, submitted to *Plant Physiology,* 1996).

The invariance of the $\mathcal{L}$ function is potentially useful in estimating the marginal increment of carbon influx through C_3 plants into terrestrial ecosystems caused by a marginal increase in atmospheric CO_2 concentration (C_a). Atmospheric CO_2 is currently increasing by about 1.5 ppm per year. Assuming that the small increase in C_a did not cause significant adjustments in leaf photosynthetic properties, the photosynthetic carbon assimilation was predicted to increase by 0.17 to 0.33% at C_a = 357 ppm in 1993 and a temperature of 20°C, for C_3 plants, regardless of growth environment associated with geographical location and canopy position [*Luo and Mooney,* 1996]. Whether or not these small incremental changes in photosynthesis are consistently constant over various spatial scales must be further tested. Mathematical analysis indicated that these small increments are additive over the global terrestrial ecosystems (appendix). Thus, the global photosynthetic carbon influx is predicted to increase by 0.18 to 0.34 Gt (1 Gt = 10^{15} g) yr^{-1} in

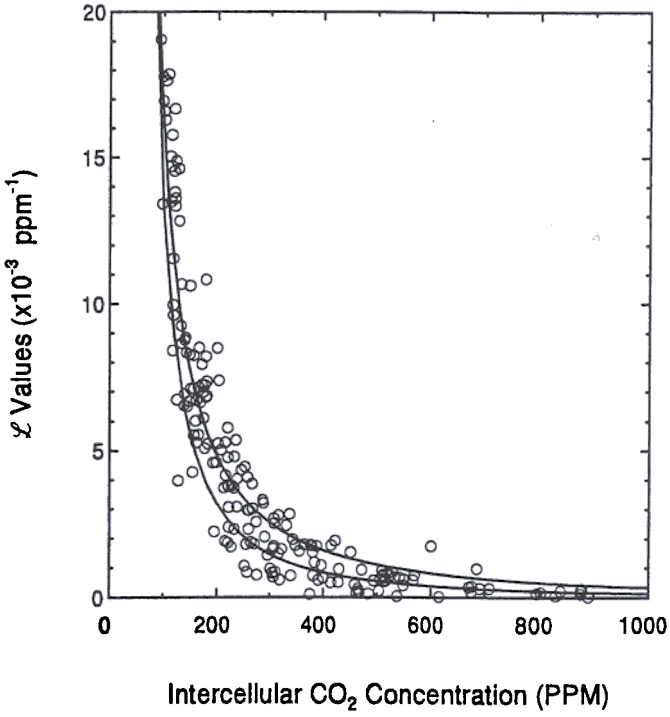

Figure 6. Values of $\mathcal{L}$ pooled from the 9 data sets with the 12 species and 8 environmental variables as plotted in Figures 1-5. Solid lines are the predicted $\mathcal{L}$ function with Γ = 45 ppm and K = 414 ppm at 25°C.

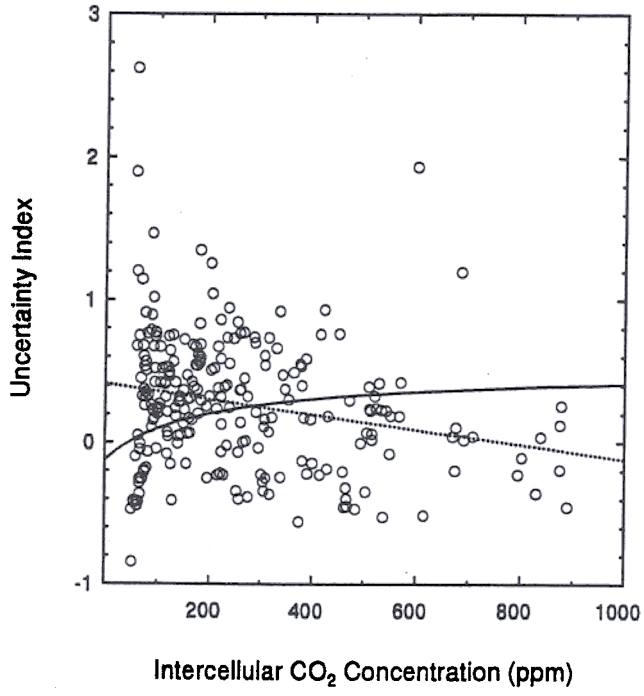

Figure 7. Theoretical (solid line) and experimental (open circles and dotted line) uncertainty indices (*UCI*) of the $\mathcal{L}$ function. Theoretical *UCI* is calculated with equations (3a), (3b), and (5) using $\Gamma = 45$ ppm and $K = 414$ ppm at 25°C. Experimental values of *UCI* (open circles) was calculated from data plotted in Figures 1-5. The dotted line is the regression line of the data points.

1993 relative to that in 1992, due to a 1.5-ppm increase in C_a [*Luo and Mooney*, 1996], assuming that $P_G = 120$ Gt yr^{-1} [*Olson et al.*, 1983] and that 85% of carbon influx into global terrestrial ecosystems is generated through C_3 plant assimilation [*Lloyd and Farquhar*, 1994]. In addition to variation in the $\mathcal{L}$ function, extrapolating the $\mathcal{L}$ function to predict ΔP_G may involve uncertainties caused by spatial variation in temperature [*Kirschbaum*, 1994] and C_a, variation in estimated P_G, low photosynthetic sensitivity of C_4 plants to C_a, and phosphate limitations of photosynthesis for some C_3 plants (see detailed discussion by *Luo and Mooney* [1996]).

Applying the $\mathcal{L}$ function across temporal scales to study long-term stimulation of carbon influx associated with a large increase in C_a requires understanding of adjustments in leaf properties, canopy structure, and vegetation redistribution as well as understanding feedback effects of ecosystem nutrient availability on photosynthetic carbon influx [*Luo and Mooney*, 1995]. Acclimation to growth at elevated CO_2 leads to highly diverse changes in leaf properties among species [*Luo et al.*, 1994]. However, synthetic analyses based on P/C_i (photosynthesis/intercellular CO_2 concentration) responses [*Sage*, 1994], photosynthetic rates of woody species [*Gunderson and Wullschleger*, 1994], meta-data analysis [*Curtis*, 1996], and nitrogen-photosynthesis relationships [*Luo and Mooney*, 1995] suggest that acclimation response is small when considered over a range of species and growth environments. Our understanding of canopy adjustment and vegetation redistribution at elevated CO_2 is highly limited [*VEMAP*, 1995]. Feedback effects of ecosystem nitrogen availability on photosynthesis can be substantially large to regulate global and regional carbon cycles in elevated CO_2 [*Comins and McMurtrie*, 1993; *Melillo et al.*, 1993]. In general, the $\mathcal{L}$ function is not able to estimate actual amount of long-term stimulation of carbon influx into terrestrial ecosystems. However, it potentially sets a boundary of the carbon influx to constrain global predictions over a long term.

The $\mathcal{L}$ function, combining the global ecosystem carbon residence time (τ_G), provides a novel approach (the $\mathcal{L}$-τ_G approach) to study global terrestrial carbon sequestration (Y. Luo, An integrated global terrestrial carbon sequestration model, submitted to *Global Biogeochemical Cycles*, 1996, hereafter referred to as Y. Luo, 1996). Existing global models predict net primary productivity of terrestrial ecosystems as regulated by nutrient, C_a, and water in each spatial grid [*Comins and McMurtrie*, 1993; *Melillo et al.*, 1993; *Potter et al.*, 1993]. Difficulties in vegetation delineation and parameterization undermine precision of global predictions which is required to be extremely high in order to quantify the terrestrial carbon sink. This $\mathcal{L}$-τ_G approach, however, focuses on a mechanism that differential increases in photosynthesis and respiration with rising C_a, caused by a time delay in respiration, possibly lead to net carbon storage in global ecosystems (Y. Luo 1996). The invariance of $\mathcal{L}$ and robust estimation of τ_G help greatly improve the precision and reduce uncertainties in global predictions. In addition the $\mathcal{L}$-τ_G approach is highly flexible to integrate other ecosystem variables into prediction of terrestrial carbon sequestration (Y. Luo, and J.F. Reynolds, A conceptual framework for studying ecosystem carbon sequestration in response to rising atmospheric CO_2 concentration, submitted to *Plant Soil*, 1996, hereafter referred to as Y. Luo and J.F. Reynolds, 1996). For example, if rising C_a reduces decomposability of litter due to increased lignin content, ecosystem residence time will be increased, leading to an increased potential of ecosystems to sequester carbon. CO_2-induced changes in ecosystem photosynthetic properties, mediated through ecosystem nitrogen availability, can be reflected by adjusting values of the $\mathcal{L}$ function (equation (A7), appendix) and then predictions of ecosystem carbon sequestration. Overall, this approach has the potential to integrate process-oriented studies of carbon dynamics into much accurate predictions of CO_2-induced carbon sequestration in terrestrial ecosystems.

In summary, CO_2 stimulation of global photosynthetic carbon influx from the atmosphere to terrestrial ecosystems can be assessed on its two components: sensitivity and acclimation. Acclimation to growth in elevated CO_2 varies with species and growth environments. Sensitivity of photosynthetic carbon influx to CO_2 concentration is an invariant function for C_3 plants despite considerable variation in photosynthetic capacity among species grown in diverse environments and despite high variability in photosynthetic rates for plants exposed to instantaneous fluctuations in light and temperature. The invariance of the $\mathcal{L}$ function enables us to cut across interspecific variation and environmental heterogeneity and thereby to provide a much accurate prediction of the short term increment in global carbon influx stimulated by a small increase in C_a. We are developing a new conceptual framework to estimate long-term changes in P_G associated with a large increase in C_a and to quantify ecosystem carbon sink by considering photosynthetic sensitivity, acclimation, and ecosystem carbon residence time.

Appendix: Mathematical Formulations of Global Photosynthetic Sensitivity and Acclimation

Annual global photosynthetic carbon influx [P_G, Gt ($=10^{15}$ g) yr^{-1}], that is, gross primary productivity, is the sum of carbon influx from total leaf area within canopies (x) over the global surface (y) over the period of a year (t) [$P(x,y,t)$, $\mu g\ m^{-2}\ s^{-1}$]. Mathematically, it can be expressed as

$$P_G = \int_{t=year} \int_{y=globe} \int_{x=canopy} P(x,y,t)\, dx\, dy\, dt \qquad \text{(A1)}$$

For simplicity, $P(x,y,t)$ is abbreviated as P hereafter. For one unit change in the global atmospheric CO_2 concentration (C_a, ppm), the rate of P_G change (Gt $ppm^{-1}\ yr^{-1}$) is

$$\frac{dP_G}{dC_a} = \iiint \frac{dP}{dC_a} dx\, dy\, dt = \iiint (\mathfrak{L} \cdot P) dx\, dy\, dt \qquad \text{(A2)}$$

where $\mathfrak{L}$ is a leaf-level function (ppm^{-1}) defined as

$$\mathfrak{L} = \frac{1}{P}\frac{dP}{dC_a} \qquad \text{(A3)}$$

The $\mathfrak{L}$ function denotes the normalized leaf photosynthetic response to one unit C_a change.

For a very small change in C_a so that acclimation is negligible, $\mathfrak{L}$ has been found to be approximately constant at given C_a for C_3 plants (the validity is discussed in this paper). Mathematically, we can move a constant $\mathfrak{L}$ directly from the inside to the outside of the triple integers in equation (A2). Thus, (A2) becomes

$$\frac{dP_G}{dC_a} = \mathfrak{L} \cdot P_G \qquad \text{(A4)}$$

Equation (A4) indicates that the rate of P_G change relative to C_a can be calculated simply from $\mathfrak{L}$ and P_G. It follows that the additional amount of annual photosynthetic carbon influx (ΔP_G, Gt yr^{-1}), stimulated by a yearly increase in atmospheric CO_2 concentration (ΔC_a), can be estimated by

$$\Delta P_G = \mathfrak{L} \cdot P_G \cdot \Delta C_a \qquad \text{(A5)}$$

For a large change in C_a over a long term so that acclimation may considerably change photosynthetic capacity, the $\mathfrak{L}$ function is modified as

$$\mathfrak{L}' = \mathfrak{L} + \frac{1}{z}\frac{dz}{dC_a} \qquad \text{(A6)}$$

where z is one of the parameters J or V_{cmax}. Consequently, the additional carbon influx are

$$\Delta P_G' = \Delta P_G + \Delta C_a \int_{t=year} \int_{y=globe} \int_{x=canopy} \left(\frac{P}{z}\frac{dz}{dC_a}\right) dx\, dy\, dt$$

The first term on the right side of (A7) is the (A5) and estimates the increment of carbon gain due to sensitivity. The second term of equation (A7) embraces concepts of photosynthetic acclimation across various scales from leaf, canopy to vegetation redistribution, and growing season shifting. The term $(P/z)(dz/dC_a)$ represents adjustments in leaf photosynthetic parameters J and V_{cmax}. The term encompassed by the most inner integer describes adjustments in canopy photosynthetic properties including changes in leaf area index and leaf properties. The term encompassed by the middle integer describes adjustments in spatial distribution of photosynthetic properties, including redistribution of vegetation and changes in leaf and canopy photosynthetic properties. The term encompassed by the outside integer describes adjustments in photosynthetically active seasons. Quantifying adjustments in these temporal and spatial scales requires comprehensive experimental and modeling studies.

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