Carbon Dioxide and Terrestrial Ecosystems

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Academic Press

San Diego New York Boston London Sydney Tokyo Toronto

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Stimulation of Global Photosynthetic Carbon Influx by an Increase in Atmospheric Carbon Dioxide Concentration

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I. Introduction

Atmospheric CO_2 concentration (C_a) is rapidly and unambiguously increasing (Siegenthaler and Sarmiento, 1993; Thorning *et al.*, 1989), rising from 280 ppm in preindustrial times to nearly 360 ppm in 1994 and possibly doubling in the next century. Rising C_a could substantially stimulate global photosynthetic carbon influx from the atmosphere to the biosphere (Allen *et al.*, 1986; Melillo *et al.*, 1993), potentially resulting in terrestrial ecosystems storing 1–2 Gt (1 Gt = 10^{15} g) of carbon per year (Tans *et al.*, 1990; Wigley and Raper, 1992; Gifford, 1994). Quantification of such stimulation on the global scale, therefore, is crucial for our understanding of global carbon cycling in a changing C_a environment.

Estimation of global photosynthetic carbon influx has been exceedingly difficult, utilizing either experimental or modeling approaches. Available techniques only allow us to make leaf-level and small-scale ecosystem measurements (Field and Mooney, 1990). Measurements on both scales indicate that photosynthetic responses to elevated CO_2 are extremely variable (Luo *et al.*, 1994; Sage, 1994). The biochemical capacity for leaf photosynthesis increases for some species and decreases for others under elevated CO_2 (Sage *et al.*, 1989; Stitt, 1991; Sage, 1994). Net ecosystem carbon assimilation in elevated CO_2 changed little in Artic tundra (Grulke *et al.*, 1990; Tissue and Oechel, 1987), but increased by 80% in salt marsh ecosystems on the Chesapeake Bay [Drake and Leadley, 1991; Drake *et al.*, 1996 (this volume)], depending on species composition and species-specific CO_2 responses

(Mooney *et al.*, 1991; Luo, 1995). Variable responses of photosynthesis at the leaf and ecosystem levels make it difficult to extrapolate small-scale studies to a global estimation of photosynthetic carbon influx.

Early modeling studies of global carbon cycling employed a single parameter, i.e., the biotic growth factor β, to account for terrestrial carbon content changes with C_a (Bacastow and Keeling, 1973). The β factor can be defined as a fractional change in net primary productivity (NPP) with a fractional change in C_a (Gates, 1985):

$$\left(\frac{\Delta NPP}{NPP}\right)\left(\frac{C_a}{\Delta C_a}\right) \tag{1}$$

Bacastow and Keeling (1973) stated that β could be as low as 0.05, but their results indicate a likely range of 0.2–0.6 based on the observed atmospheric increase from 1959 to 1969 (Gates, 1985). Amthor and Koch (1996, this volume), by using a different formulation for β, conclude from the scant experimental data available that β (NPP) is probably greater than zero in many ecosystems, but acknowledge a very wide range of values between, and even within, ecosystems. Limited understanding of the biological basis of the β factor circumscribes its applications in global carbon cycling studies (Harvey, 1989).

Modeling studies have integrated more biological information into predicting global terrestrial carbon exchanges (Prentice and Fung, 1990; Smith *et al.*, 1992; Melillo *et al.*, 1993; Potter *et al.*, 1993). These models usually use geographical maps of world vegetation and soils and characteristic parameters of each vegetation and soil type. CO_2 effects on carbon uptake are generally based on experimental results at the leaf or small ecosystem scales (Melillo *et al.*, 1993). Environmental heterogeneity in global ecosystems and diverse species characteristics, however, still hinder our understanding of CO_2 influences on carbon fluxes between the biosphere and atmosphere.

Here we have employed an analytical approach in an attempt to overcome difficulties associated with environmental heterogeneity and species characteristics in studying global photosynthetic carbon influx. We examine leaf photosynthesis, focusing on its relative response to a small change in atmospheric CO_2 concentration (the leaf-level $\mathcal{L}$ factor). From simple mathematical manipulations of a mechanistic model of leaf photosynthesis (Farquhar *et al.*, 1980), we find that the $\mathcal{L}$ factor is an approximate constant for any C_3 plant, regardless of the geographical location and canopy position. We explore the biochemical basis of the $\mathcal{L}$ factor being an approximate constant and discuss the possibility of extrapolating the $\mathcal{L}$ factor across spatial and temporal scales to estimate the additional amount of global photosynthetic carbon influx (P_G) stimulated by a small C_a increase. We also develop a relationship between the $\mathcal{L}$ factor and the biotic growth factor β.

II. The Model

Annual global photosynthetic carbon influx [P_G, Gt ($=10^{15}$g) yr^{-1}], i.e., 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) [$P(x,y,t)$, g m^{-2} s^{-1}]. Mathematically, it can be expressed as

$$P_G = \int_{t=\text{year}} \int_{y=\text{globe}} \int_{x=\text{canopy}} P(x, y, t)\, dx\, dy\, dt \tag{2}$$

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

$$\begin{aligned}\frac{dP_G}{dC_a} &= \iiint \frac{dP}{dC_a}\, dx\, dy\, dt \\ &= \iiint (\mathcal{L}P)\, dx\, dy\, dt\end{aligned} \tag{3}$$

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

$$\mathcal{L} = \frac{1}{P}\frac{dP}{dC_a} \tag{4}$$

The $\mathcal{L}$ factor denotes the relative leaf photosynthetic response to a 1 ppm C_a change.

The vast majority of all terrestrial plants share a C_3 photosynthetic pathway (Bowes, 1993). Leaf photosynthesis of C_3 plants, which is usually limited either by electron transport or by ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco) activity, is predicted by the well-established Farquhar *et al.* (1980) model. When photosynthesis is limited by electron transport, leaf photosynthetic carbon influx (P_l) is

$$P_l = J\frac{C_i - \Gamma}{4.5C_i + 10.5\Gamma} \tag{5}$$

where J is the electron transport rate (μmol m^{-2} s^{-1}), C_i is the intercellular CO_2 concentration (ppm), and Γ is the CO_2 compensation point without dark respiration (ppm). With the assumption that C_i is proportional to C_a as,

$$C_i = \alpha C_a, \quad 0 < \alpha < 1, \tag{6}$$

the corresponding $\mathcal{L}$ factor is

$$\mathcal{L}_l = \frac{15\alpha\Gamma}{(\alpha C_a - \Gamma)(4.5\alpha C_a + 10.5\Gamma)} \tag{7}$$

Parameter J is eliminated from Eq. (7) because $\mathcal{L}_l$ is a measure of relative response.

When photosynthesis is limited by rubisco activity, leaf carbon influx (P_2) is

$$P_2 = V_{cmax}\frac{C_i - \Gamma}{C_i + K} \tag{8}$$

where V_{cmax} is the maximum carboxylation rate (μmol m^{-2} s^{-1}) and K is a coefficient (ppm) associated with enzyme kinetics. The corresponding $\mathcal{L}$ factor is

$$\mathcal{L}_2 = \frac{\alpha(K+\Gamma)}{(\alpha C_a - \Gamma)(\alpha C_a + K)} \tag{9}$$

Parameter V_{cmax} is eliminated from Eq. (9) because $\mathcal{L}_2$ is also a measure of relative response. Because the physiological process of electron transport is less sensitive to CO_2 concentration than is carboxylation, $\mathcal{L}_1$ and $\mathcal{L}_2$ define the lower and upper limits, respectively, of the $\mathcal{L}$ factor.

Equations (7) and (9) suggest that both the lower and upper limits of the $\mathcal{L}$ factor are independent of the light-related parameter J and enzyme-related parameter V_{cmax} and vary with C_a, α, Γ, and K. With the assumption that the four parameters are constant (the validity is discussed in the following), the $\mathcal{L}$ factor is a constant regardless of plant species, vertical position in a canopy, geographical location on the earth, and time of year. Thus, Eq. (3) becomes

$$\frac{dP_G}{dC_a} = \mathcal{L}P_G \tag{10}$$

Equation (10) indicates that the rate of P_G change relative to C_a can be calculated simply from $\mathcal{L}$ 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

$$\begin{aligned}\Delta P_{G,1} &= \mathcal{L}_1 P_G \Delta C_a \\ \Delta P_{G,2} &= \mathcal{L}_2 P_G \Delta C_a\end{aligned} \tag{11}$$

where $\Delta P_{G,1}$ and $\Delta P_{G,2}$ are the lower and upper limits of ΔP_G, respectively. When the photosynthesis of global vegetation is mainly limited by light, biochemical processes related to electron transport limit photosynthesis, and the additional global photosynthetic carbon influx is close to the lower limit. Otherwise, it may approach the upper limit.

III. Results and Discussion

A. Relative Photosynthetic Response to CO_2 ($\mathcal{L}$ Factor)

Photosynthesis in the light-limited environment increases by 0.183% ($\mathcal{L}_1$) for C_a at 280 ppm, 0.115% at 357 ppm, and 0.077% at 440 ppm (Fig. 1),

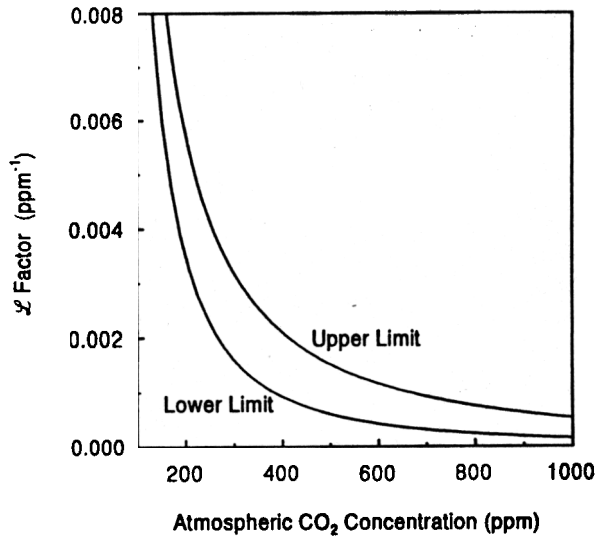

Figure 1 Lower ($\mathcal{L}_1$) and upper ($\mathcal{L}_2$) limits of the $\mathcal{L}$ factor (relative leaf photosynthetic response to a 1-ppm CO_2 change) within a range of atmospheric CO_2 concentrations from 100 to 1000 ppm, predicted by Eqs. (7) and (9) with $\alpha = 0.70$, $\Gamma = 35$ ppm, and $K = 650$ μmol m^{-2} s^{-1}.

with $\alpha = 0.70$ and $\Gamma = 35$ ppm when the atmospheric CO_2 concentration (C_a) increases by 1 ppm [Eq. (7)]. In the enzyme-limited condition, photo synthesis increases by 0.352% ($\mathcal{L}_2$) for C_a at 280 ppm, 0.248% at 357 ppm, and 0.183% at 440 ppm (Fig. 1), with $\alpha = 0.70$, $\Gamma = 35$ ppm, and $K = 650$ ppm due to a 1-ppm CO_2 increase [Eq. (9)].

Relative photosynthetic response to CO_2 (the $\mathcal{L}$ factor) varies with parameters, α, Γ, and K. The C_i/C_a ratio (α) is sensitive to water status and CO_2 concentration but fairly constant among species when plants grow in their natural environments (Pearcy and Ehleringer, 1984; Evans and Farquhar, 1991). When α decreases by 0.10 from 0.70, $\mathcal{L}_1$ increases by 15% and $\mathcal{L}_2$ by 7% (Fig. 2A). When α increases by 0.10, $\mathcal{L}_1$ decreases by 12% and $\mathcal{L}_2$ by 6%. The CO_2 compensation point (Γ) varies little among species, but depends strongly on temperature (Jordan and Ogren, 1984; Brooks and Farquhar, 1985). A value of $\Gamma = 35$ ppm chosen here corresponds to that at 20°C, which is about 4°C higher than the average earth surface temperature (Schlesinger, 1991) to account for most photosynthetic machinery distributed in warmer tropic and temperate zones. As globally averaged temperature changes by ±5°C, leading to approximately ±7 ppm changes in Γ from 35 ppm, $\mathcal{L}_1$ varies by 19% and $\mathcal{L}_2$ by 4% (Fig. 2B). The enzyme kinetic parameter K is variable among species (Evans and Seemann, 1984; Harley

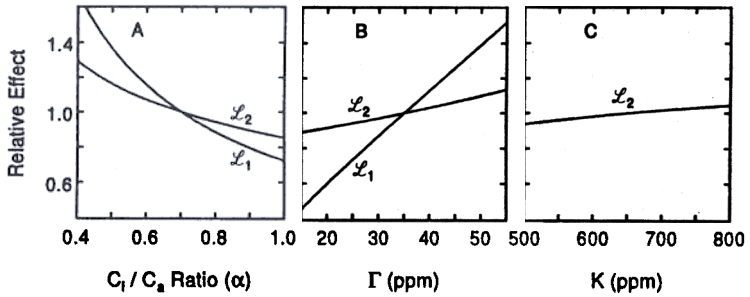

Figure 2 Effects of (A) C_i/C_a ratio (α), (B) Γ (CO_2 compensation point), and (C) K (enzyme kinetic parameter) on the lower and upper limits of $\mathcal{L}$. Parameter values are the same as in Fig. 1.

and Tenhunen, 1991), but only slightly affects the upper limit of the $\mathcal{L}$ factor (Fig. 2C).

The Farquhar *et al.* (1980) model describes two general biochemical processes of leaf photosynthesis: ribulose 1,5-bisphosphate (RuBP) regeneration driven by light and carbon fixation catalyzed by ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco). Effects of light, nutrient availability, and plant characteristics on photosynthesis are reflected by variations in J and V_{cmax} values, and the values of these two parameters vary greatly (Wullschleger, 1993). Parameter V_{cmax} ranges from 6 μmol m^{-2} s^{-1} for the coniferous species *Picea abies* (Benner *et al.*, 1988) to 194 μmol m^{-2} s^{-1} for the agricultural species *Beta vulgaris* (Taylor and Terry, 1984) and averages 64 μmol m^{-2} s^{-1} for 109 species (Wullschleger, 1993). Parameter J increases with light in a rectangular hyperbolic shape and reaches a maximum, J_{max} (Farquhar *et al.*, 1980). The latter also varies greatly among species (Wullschleger, 1993). Both V_{cmax} and J_{max} vary with nutrient availability (Field, 1983; Harley *et al.*, 1992). Our mathematical derivation eliminates parameters J and V_{cmax}, leading to the $\mathcal{L}$ factor being independent of plant characteristics, light, and nutrient environment. The resultant $\mathcal{L}$ factor is only a function of α, Γ, K, and C_a. Since α, Γ, and K only slightly affect the $\mathcal{L}$ factor (Fig. 2), and C_a varies little over different geographical locations (Conway and Tans, 1989) and canopy positions (Monteith and Unsworth, 1990), the $\mathcal{L}$ factor is virtually a constant across ecosystems, but a function of time-associated changes in C_a.

B. Biochemical Basis of the $\mathcal{L}$ Factor

That the $\mathcal{L}$ factor is an approximate constant at a given C_a is rooted in the nature of the biochemical reactions of photosynthesis. Photosynthesis (i.e., carboxylation of RuBP) and photosrespiration (i.e., oxygenation of RuBP) are both catalyzed by rubisco (Andrews and Lorimer, 1987). The

rubisco reaction with molecular carbon dioxide via carboxylation of RuBP leads to carbohydrate synthesis in the photosynthetic carbon reduction (PCR) cycle (Fig. 3). The rubisco reaction with molecular oxygen via oxygenation of RuBP leads to carbohydrate anabolism in the photorespiratory carbon oxidation (PCO) cycle with resultant release of CO_2 (Fig. 3). An increased CO_2 concentration competes with O_2 and decreases the oxygenase activity of rubisco (Farquhar *et al.*, 1980; Stitt, 1991; Lawlor, 1993), leading to an increased ratio of carboxylation to oxygenation.

The carboxylation acceptor, RuBP, is regenerated in the PCR cycle, which is driven by light energy. When light limits photosynthesis, regeneration of RuBP controls the photosynthetic rate (Farquhar *et al.*, 1980). With a certain amount of regenerated RuBP, a portion of RuBP binds molecular carbon dioxide in the PCR cycle to produce carbohydrate, and a portion of RuBP is used to bind molecular oxygen to release CO_2 in the PCO cycle (Fig. 3). Despite different light levels, leading to different electron transport rates and regeneration rates of RuBP (von Caemmerer and Edmonson, 1986; Andrew and Lorimer, 1988; Sage *et al.*, 1990), light does not change the fraction of RuBP involved in carboxylation versus oxygenation. An increasing CO_2 concentration does not change the regeneration rates of RuBP, but increases the portion of RuBP for carboxylation in the PCR cycle and decreases the portion of RuBP for oxygenation in the PCO cycle. Carboxylation efficiency (carboxylation rate per unit of photosynthetic machinery) increases. Thus, the relative photosynthetic response to CO_2 (the $\mathcal{L}$ factor) is not dependent on RuBP regeneration rate and light level, but is dependent on changes in CO_2 concentration.

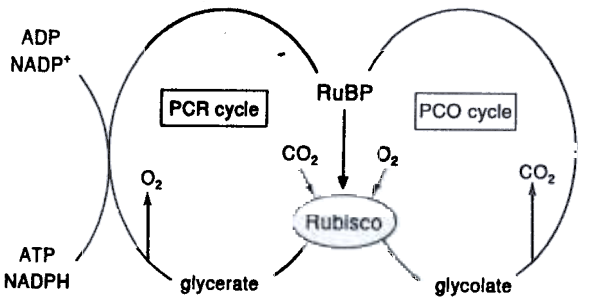

Figure 3 Illustration of the biochemical reaction of photosynthesis. Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) catalyzes both the carboxylation and oxygenation of RuBP (ribulose 1,5-bisphosphate). RuBP reacts with CO_2 (carboxylation) in the photosynthetic carbon reduction (PCR) cycle to produce carbohydrate and with O_2 (oxygenation) in the photorespiratory carbon oxidation (PCO) cycle to release CO_2. RuBP is regenerated in the PCR cycle, consuming energy and electrons generated in light reactions. The ratio of carboxylation to oxygenation (the $\mathcal{L}$ factor) is regulated by the CO_2/O_2 ratio and temperature, but is independent of light-driven regeneration of RuBP and plant-specific content of rubisco.

When light does not limit photosynthesis and RuBP is saturated, rubisco controls the photosynthetic rate (Farquhar *et al.*, 1980). With a fixed amount of rubisco, a portion of rubisco binds molecular carbon dioxide to produce carbohydrate in the PCR cycle, and a portion of rubisco binds molecular oxygen to release CO_2 in the PCO cycle (Fig. 3). A small increase in C_a does not change the rubisco amount, but increases the fraction of rubisco binding with molecular carbon dioxide and decreases the portion of rubisco binding molecular oxygen. It follows that the relative photosynthetic response to CO_2 (the $\mathcal{L}$ factor) is independent of rubisco content but varies with the CO_2 concentration.

The ability of rubisco to bind CO_2 versus O_2, i.e., the CO_2/O_2 specificity of rubisco, depends on temperature (Farquhar *et al.*, 1980; Jordan and Ogren, 1984). This temperature dependence is reflected in the CO_2 compensation point (G), which slightly influences the $\mathcal{L}$ factor (Fig. 2B). Although plant water status influences the CO_2/O_2 ratio at the reaction sites, homeostatic adjustments through photosynthetic rate and stomatal opening lead to a fairly constant intercellular CO_2 concentration and CO_2/O_2 ratio (Pearcy and Ehleringer, 1984; Evans and Farquhar, 1991). Thus, parameter $\alpha(= C_i/C_a)$ varies within a narrow range and slightly affects the $\mathcal{L}$ factor. In short, a small increase in atmospheric CO_2 leads to an increase in CO_2/O_2, the carboxylation/oxygenation ratio, and the rate of carboxylation, the fractional increase of which (the $\mathcal{L}$ factor) is independent of light-driven regeneration of RuBP (J) and plant-specific content of rubisco (V_{cmax}), is slightly influenced by temperature and water stress.

C. Spatial Extrapolation of the $\mathcal{L}$ Factor to the Global Scale

Mathematical derivation and biochemical examination both indicate that the relative photosynthetic response to CO_2 (the $\mathcal{L}$ factor) is independent of light, nutrient environment, and species characteristics, but is a function of atmospheric CO_2 concentration and is slightly influenced by temperature and water. This property of the $\mathcal{L}$ factor provides the possibility of extrapolating the leaf-level $\mathcal{L}$ factor to the global scale for estimating the additional P_G stimulated by C_a increase. Indeed, small-scale measurements can be extrapolated to the global scale, provided that the parameter in question is an approximate constant relative to environmental and biological variables. An example is atmospheric CO_2 concentration, which is independent of temperature, moisture, and other atmospheric factors and is only slightly influenced by biospheric activities, i.e., an approximate constant across spatial scales at a given time.

Along with the approximate global constancy of C_a, several other factors make it possible to extrapolate the $\mathcal{L}$ factor across spatial scales to estimate carbon influx from the atmosphere to the biosphere. First, photosynthesis is the almost exclusive pathway through which terrestrial ecosystems take up carbon from the atmosphere (Mooney *et al.*, 1987). Second, the vast majority of plants in terrestrial ecosystems share the C_3 photosynthetic pathway (Bowes, 1993). Third, photosynthesis of C_3 plants can be well described by the Farquhar *et al.* (1980) model. Since the $\mathcal{L}$ factor is derived simply from the Farquhar model, its approximate constancy at a given C_a propagates to the majority of terrestrial plants in the earth system.

Additional global photosynthetic carbon influx estimated from extrapolating the $\mathcal{L}$ factor to the global scale [Eq. (11)] is between 0.21 and 0.45 Gt yr^{-1} in 1993 compared to that in 1992 (Fig. 4), with C_a = 357 ppm, ΔC_a = 1.5 ppm (Thorning *et al.*, 1989), and P_G = 120 Gt yr^{-1} (Olson *et al.*, 1983). Stimulation of global carbon influx by increasing C_a diminishes from 0.25 in 1970 to 0.17 Gt yr^{-1} in 2020 for the lower limit and from 0.52 to 0.38 Gt yr^{-1} for the upper limit during the same period (Fig. 4), if C_a increases by 1.5 ppm each year.

The predicted ΔP_G varies with α, Γ, and K in a parallel manner for the $\mathcal{L}$ factor (Fig. 2). In addition, C_a over different geographical locations and at different positions in a canopy generally varies by less than 20 ppm (Conway and Tans, 1989; Monteith and Unsworth, 1990). Thus, global variations of CO_2 concentration at leaf surfaces may be much less than 40 ppm. That would cause a slight change in the estimated ΔP_G. Although CO_2 concentration in the forest floor may be as high as 420 ppm (Bazzaz

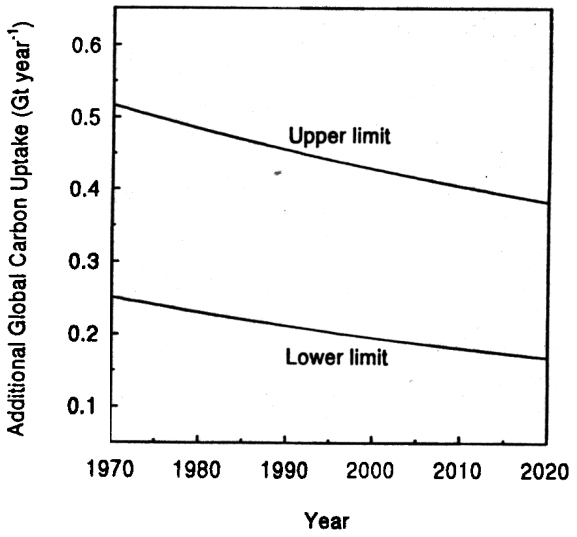

Figure 4 Lower ($\Delta P_{G,1}$) and upper ($\Delta P_{G,2}$) limits of the additional amount of global photosynthetic carbon influx stimulated by a 1.5-ppm increase in atmospheric CO_2 concentration per year, predicted by Eq. (11) with α = 0.70, Γ = 35 ppm, K = 650 ppm, P_G = 120 Gt yr^{-1}, and ΔC_a = 1.5 ppm.

and Williams, 1991), its effect on ΔP_G is negligible because understory plants contribute little to P_G. Estimated P_G varies by 20–30 Gt yr^{-1} (Olson, *et al.*, 1983). When a different P_G is used, ΔP_G could vary by up to 20%. The additional carbon influx (ΔP_G) could be slightly lowered by the presence of C_4 plants, whose photosynthesis is less sensitive to C_a change than the C_3 species (Collatz *et al.*, 1992), and some C_3 plants, whose photosynthesis is limited by phosphate regeneration, which desensitizes the CO_2 response (Sharkey, 1985; Wullschleger, 1993).

D. Applying the $\mathcal{L}$ Factor for Long-Term Studies

Our model predicts additional global photosynthetic carbon influx induced by a small increase in C_a. The prediction is based on the assumption that a few ppm CO_2 change in the atmosphere does not alter parameters J and V_{cmax}. Plants grown under twice the current ambient CO_2 concentration, however, have shown both increases and decreases in photosynthetic capacity (see, for example, Sage *et al.*, 1989; Wong, 1990; Ryle *et al.*, 1992). Changes in photosynthetic capacity result from variations in J_{max} (the maximum J) and V_{cmax}. When J and V_{cmax} vary with CO_2 concentration, the $\mathcal{L}$ factor is modified as

$$\mathcal{L}_1' = \mathcal{L}_1 + \frac{1}{J}\frac{dJ}{dC_a}$$
$$\mathcal{L}_2' = \mathcal{L}_2 + \frac{1}{V_{cmax}}\frac{dV_{cmax}}{dC_a} \qquad (12)$$

Consequently, the lower and upper limits of the additional carbon influx are

$$\Delta P'_{G,1} = \Delta P_{G,1} + \Delta C_a \int\int\int \left(\frac{P}{J}\frac{dJ}{dC_a}\right) dx\, dy\, dt$$
$$\Delta P'_{G,2} = \Delta P_{G,2} + \Delta C_a \int\int\int \left(\frac{P}{V_{cmax}}\frac{dV_{cmax}}{dC_a}\right) dx\, dy\, dt \qquad (13)$$

Equation 13 indicates that, if globally averaged J and V_{cmax} decrease by 10% in the 700-ppm CO_2 concentration in comparison to those in 350 ppm, $\Delta P_G'$, on average, should be smaller by 0.0514 Gt yr^{-1} than ΔP_G, with P_G = 120 Gt yr^{-1} and ΔC_a = 1.5 ppm each year. If globally averaged J and V_{cmax} increase by 10% in the 700-ppm CO_2 concentration, $\Delta P_G'$ on average, should be larger by 0.0514 Gt yr^{-1} than ΔP_G.

Two reviews reveal that leaf photosynthetic capacity aggregated across a variety of species varies little with CO_2 (Sage, 1994; Luo, 1995). Based on theoretical interpretations of A/C_i (assimilation versus intercellular CO_2 concentration) curves, Sage (1994) concluded that growth in elevated CO_2 leads to a higher photosynthetic capacity than in ambient CO_2 for 12 out

of 27 species with plants grown in pots and for 2 out of 3 species with plants grown in the field. Luo (1995) used nitrogen–photosynthesis relationships (Field, 1983; Harley *et al.*, 1992) and predicted that J_{max} and V_{cmax} decreased by 2.1% for all 33 species surveyed from published papers, by 4.1% for a subgroup of 11 crop species, and by 1.1% for a subgroup of 22 wild species with a doubled CO_2. Although ecosystem carbon fluxes depend on canopy structure, effects of elevated CO_2 on canopy development are largely unknown (Luo and Mooney, 1995).

With the assumption that globally averaged J and V_{cmax} do not change with C_a, the $\mathcal{L}$ factor can be directly used to estimate cumulative additional carbon influx. The atmospheric CO_2 concentration increased by 42 ppm from 1958 to 1993. That results in 5.6–12.1% more carbon influx in 1993 than in 1958, equaling an additional 6.7–14.5 Gt yr^{-1} with P_G = 120 Gt yr^{-1} (Table I). A 77-ppm C_a increase from preindustrial times to 1993 could stimulate global carbon influx by 11.8–25.5%. Doubling of C_a from 350 to 700 ppm would lead to a 23.8–70.1% increase in global photosynthetic carbon influx (Table I).

Use of the $\mathcal{L}$ factor to estimate the long-term stimulation of global carbon influx by a cumulative C_a increase requires caution due to two major issues. One is the possibility of CO_2-induced adjustments in leaf and ecosystem photosynthetic properties and, thus, the parameters V_{cmax} and J_{max}. The other is the degree of limitation of global photosynthetic stimulation and global NPP by nutrient limitation under rising CO_2 (Luo and Mooney, 1995). Limited evidence supports the idea that the parameters V_{cmax} and J_{max}, averaged across a group of species, vary little with CO_2 concentration. We recognize, however, that this is based largely on data for herbaceous species, whereas most of the global terrestrial carbon fixation is by long-lived woody species, for which there is limited data. The second, and related, point of caution concerns the influence of elevated CO_2 on interactions between the carbon and nitrogen cycles (Johnson *et al.*, 1996, O'Neill and Norby, 1996, and Curtis *et al.*, 1996, all in this volume) and the role of nitrogen deposition from the atmosphere in meeting increased nitrogen demand under elevated CO_2 (Schindler and Bayley, 1993; Hudson *et al.*,

Table I Changes in Global Photosynthetic Carbon Influx in Four Periods of Time

Period	ΔC_a (ppm)	ΔP_G (%)	ΔP_G[a] (Gt yr^{-1})
1992–1993		0.17–0.37	
1958–1993		5.6–12.1	
Preindustrial times to 1993		11.8–25.5	
1988 to 21st century		23.8–70.1	

[a] With P_G = 120 Gt yr^{-1} (1 Gt = 10^{15} g).

1994). At this time, uncertainties in these areas only serve to emphasize the tentative nature of our conclusions regarding the long-term stimulation of carbon influx by a cumulative increase in C_a.

E. Photosynthetic β Factor Defined from the $\mathcal{L}$ Factor

The $\mathcal{L}$ factor developed here can be used to define the photosynthetic β factor (β_p) as

$$\beta_p = C_a\mathcal{L} = \left(\frac{dP}{P}\right)\left(\frac{C_a}{dC_a}\right) \tag{14}$$

The lower and upper limits of β_p are 0.51 and 0.99, respectively, when C_a is at 280 ppm, 0.41 and 0.89 at 357 ppm, and 0.22 and 0.65 at 700 ppm (Fig. 5). The prediction is consistent with observed data for numerous species (Fig. 5). All of the 18 data points from 5 species are within the predicted lower and upper limits.

Equation (14) is similar to Eq. (1). In Eq. (1), the growth factor β represents biomass production changes against C_a changes (Bacastow and Keeling, 1973), whereas β_p in Eq. (14) describes photosynthesis changes against C_a changes. Indeed, the growth β factor is closely related to β_p

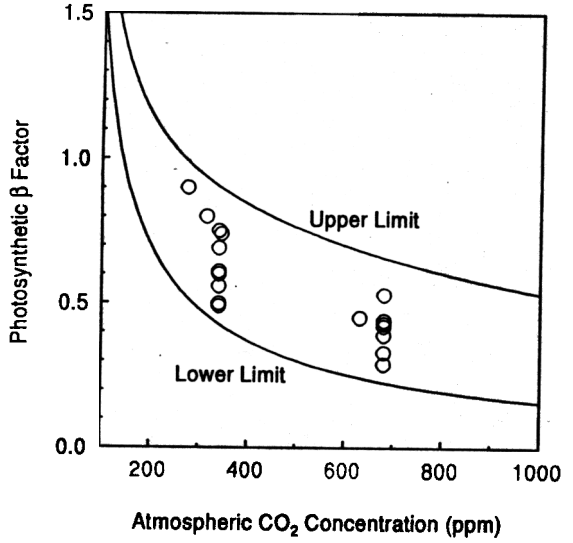

Figure 5 Lower and upper limits of photosynthetic β factor within a range of atmospheric CO_2 concentrations from 100 to 1000 ppm, predicted by Eq. (14) with $\alpha = 0.70$, $\Gamma = 35$ ppm, and $K = 650$ ppm. Symbols represent data from species *Acer saccharum* (Jurick *et al.*, 1985), *Glycine max* (Allen *et al.*, 1986), *Populus deltoides* (Regehr *et al.*, 1975), and *Populus grandidentata* and *Quercus rubra* (Jurik *et al.*, 1985).

(Gates, 1985; Allen *et al.*, 1986). Measured β (growth) for *Glycine max* was about 15% lower than measured β_p (Allen *et al.*, 1986). Values of β used in a global carbon cycling model by Bacastow and Keeling (1973) ranged from 0.2 to 0.6 for the observed C_a increase from 1959 to 1969. Goudriaan and Ketner (1984) used a β value of 0.5 to model the observed C_a increase from 1958 to 1980. Gifford (1980) found a β value of 0.6 to be necessary in his global carbon model. Those values of the growth β factor are well within the range of the photosynthetic β factor predicted from the $\mathcal{L}$ factor. A close match between values of the growth β factors used in various global carbon cycling models and predicted β_p ($\mathcal{L}C_a$) provides more support for the global application of the $\mathcal{L}$ factor.

IV. Summary

We have used leaf-level physiology to estimate the additional amount of global terrestrial carbon influx (P_G) stimulated by an increase in the atmospheric CO_2 concentration (C_a). We examined leaf photosynthesis (P), focusing on its relative response to a small change in C_a [$=dP/(PdC_a)$]. Although the response of P to C_a (dP/dC_a) varies greatly with light, nutrients, and species, normalization of dP/dC_a against P eliminates their effects. As a result, the leaf-level $\mathcal{L}$ factor is independent of light, nutrient environment, and species characteristics of C_3 plants, but rather is a function of C_a and is slightly influenced by temperature and water. Since the $\mathcal{L}$ factor is derived simply from the Farquhar *et al.* (1980) model, which predicts the photosynthesis of C_3 plants, which are the vast majority of terrestrial plants in global ecosystems, its property of being an approximate constant at a given C_a propagates to the majority of terrestrial plants in the earth system. Thus, we are able to extrapolate from the $\mathcal{L}$ factor to estimate the additional amount of P_G as stimulated by a small C_a increase. That is, 0.21–0.45 Gt ($=10^{15}$ g) yr^{-1} with $P_G = 120$ Gt yr^{-1} in 1993, compared with that in 1992, due to a 1.5-ppm C_a increase in 1993. Application of the $\mathcal{L}$ factor for long-term studies is valid when ecosystem photosynthetic properties do not change with C_a and increased carbon assimilation can be matched by nutrient supply through aerial deposition or perhaps increased nutrient use efficiency. Limited available data substantiate these two prerequisites. In this case, P_G increases by 11.8–25.5% for a 77-ppm C_a increase from preindustrial times to 1993 and by 23.8–70.1% for a C_a increase from 350 to 700 ppm. In addition, we defined the product $\mathcal{L}C_a$ as a *photosynthetic* β factor (β_p). Values of the biotic growth β factor used in a variety of global carbon cycling models are well within the predicted β_p range.

Appendix

A list of symbols and abbreviations.

Name	Description
C_a	Atmospheric CO_2 concentration
C_i	Intercellular CO_2 concentration
J	Electron transport rate
J_{max}	Maximum electron transport rate
K	Coefficient associated with enzyme kinetics
$\mathcal{L}$	Relative photosynthetic responses to 1-ppm CO_2 change
$\mathcal{L}_1$	Lower limit of $\mathcal{L}$
$\mathcal{L}_2$	Upper limit of $\mathcal{L}$
NPP	Net primary productivity
P	Photosynthetic rate
P_1	Photosynthetic rate with limitation of electron transport
P_2	Photosynthetic rate with limitation of rubisco activity
P_G	Global photosynthetic carbon influx
$P_{G,1}$	Lower limit of P_G
$P_{G,2}$	Upper limit of P_G
PCR	Photosynthetic carbon reduction
PCO	Photorespiratory carbon oxidation
rubisco	Ribulose-1,5-bisphosphate carboxylase/oxygenase
RuBP	Ribulose 1,5-bisphosphate
V_{cmax}	Maximum carboxylation rate
α	Ratio of intercellular to ambient CO_2 concentration
β	Biota growth factor
β_p	Biota photosynthetic factor
Γ	CO_2 compensation point

Acknowledgments

We thank G. D. Farquhar, C. B. Field, P. M. Vitousek, R. S. Loomis, F. S. Chapin, III, and G. W. Koch for their suggestions and comments. This work is supported by a grant from the National Science Foundation (BSR-90-20347).

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