Long-term CO₂ stimulation of carbon influx into global terrestrial ecosystems: issues and approaches

YI QI LUO* and HAROLD A. MOONEY† *Biological Sciences Center, Desert Research Institute, University of Nevada System, P.O. Box 60220, Reno, NV 89512, U.S.A. and †Department of Biological Sciences, Stanford University, Stanford, CA 94305, U.S.A.

Abstract. Estimating the additional amount of global photosynthetic carbon influx into terrestrial ecosystems (PG) becomes possible with a leaf-level factor (L) developed by Luo & Mooney only when an increase in atmospheric CO₂ concentration (Ca) is small. Applying the L factor to study long-term stimulation of PG with a large increase in Ca needs understanding of adjustments in leaf properties, canopy structure and ecosystem nitrogen availability, which could, potentially, feedback to photosynthetic carbon influx. Leaf photosynthetic properties vary greatly with elevated CO₂ among species. Aggregation over a group of species, however, shows a small change, suggesting that globally averaged changes in leaf properties may be trivial. Canopy adjustment in elevated CO₂ is largely unknown whereas indirect measurements suggest faster development of foliar canopy in elevated than ambient CO₂. Biogeochemical feedback of nitrogen on global carbon influx is involved with two general issues: CO₂ effects on ecosystem nitrogen availability and interactive effects of nitrogen and CO₂ on photosynthesis. Although nitrogen itself strongly influences photosynthesis, regulation of CO₂ effects on photosynthesis by nitrogen is still inconclusive. Ecosystem nitrogen availability is determined by a balance of several nitrogen fluxes, including plant uptake, mineralization, deposition, fixation, denitrification, volatilization and leaching. Elevated CO₂ stimulates more plant biomass growth, demanding more nitrogen uptake. Mineralization increased in two studies, decreased in one and was unchanged in one. CO₂ stimulation of nitrogen fixation increases nitrogen availability in ecosystems, potentially to match increased photosynthetic potential in the long term. Effects of volatilization, denitrification and leaching are yet to be assessed. Overall, intact ecosystem studies of canopy structure and nitrogen dynamics in elevated CO₂ are particularly needed for our quantifying long-term stimulation of global photosynthetic carbon influx.

Key words. Biogeochemical cycles, canopy, ecosystems, feedback, leaf, model, nitrogen.

INTRODUCTION

Atmospheric CO₂ concentration is rapidly and unambiguously increasing (Siegenthaler & Sarmiento, 1993; Thornton, Tans & Komhyr, 1989), rising from 280 p.p.m. in pre-industrial times to nearly 360 p.p.m. in 1994 and doubling in the next century. Rising Ca could substantially stimulate global photosynthetic carbon influx (Allen et al., 1986; Melillo et al., 1993). Since photosynthesis is the primary pathway through which terrestrial ecosystems take up carbon inward from the atmosphere (Mooney, Vitousek & Matson, 1987), an increase in photosynthetic carbon influx will lead to a suite of changes in terrestrial carbon processes. Increased carbohydrate supply, for example, generally enhances plant biomass growth and more carbon is translocated to soils. The additional carbon to the soils could either be respired back to the atmosphere, incorporated into soil carbon pools, or both. Stimulation of respiration will accelerate the terrestrial carbon cycling and increase carbon turnover rate. Incorporation of the additional carbon into the passive carbon pool will lead to net soil carbon storage. In short, stimulation of photosynthetic carbon influx by an increase in atmospheric CO₂ concentration drives changes in the biogeochemical carbon cycle. Estimating such stimulation is crucial for our understanding of the global carbon balance.

Estimation of the additional amount of global photosynthetic carbon influx (PG) stimulated by a small increase in atmospheric CO₂ concentration (Ca) becomes possible with a leaf-level factor \( L = \frac{dP}{dC_a} \) (where \( P \) is leaf photosynthesis) (Luo & Mooney, 1995). Although photosynthetic response to a \( C_a \) change \( \frac{dP}{dC_a} \) greatly varies with the light, water, nutrient environment and species characteristics, normalization of \( \frac{dP}{dC_a} \) against \( P \) eliminates their effects, leading to the \( L \) factor being an approximate constant at a given \( C_a \). Thus, the \( L \) factor can cut across spatial scales to estimate the global photosynthetic carbon influx when a change in \( C_a \) is small enough.

Applying the \( L \) factor to study long-term stimulation of \( P_a \) by a large increase in \( C_a \) needs understanding of possi-
ible adjustments in leaves, canopy and nutrient supply. When the \( C_a \) change is small enough the response of photosynthetic carbon influx is primary, whereas secondary effects of increased carbon supply on leaf growth, canopy development and ecosystem nutrient dynamics are small enough to be negligible. Long-term growth in the CO\(_2\)-enriched environment, however, could alter substantially leaf photosynthetic properties, canopy structure and biogeochemistry of nutrient cycling, which feedback to photosynthetic response to \( C_a \). The main objective of this paper is to review issues involved in long-term studies of global photosynthetic carbon influx as atmospheric CO\(_2\) concentration increases. We will also propose some possible approaches to address these issues. Specifically, we will review the \( \mathcal{L} \) factor and examine adjustments in leaf photosynthetic properties and canopy development. Effects of nitrogen on photosynthetic adjustments and biogeochemical feedback effects on ecosystem nitrogen availability will be discussed. Global carbon influx could also be affected by land use change (Meyer & Turner, 1992) and shifting the vegetation distribution (Prentice & Fung, 1990), which are beyond the scope of this paper.

**REVIEW OF THE \( \mathcal{L} \) FACTOR**

The \( \mathcal{L} \) factor is an approximate constant at a given \( C_a \) which provides a possibility to estimate the additional amount of global photosynthetic carbon influx. Luo & Mooney (1995) derived the \( \mathcal{L} \) factor from the well-established Farquhar, von Caemmerer & Berry (1980) model. Leaf photosynthesis of \( C_3 \) plants is usually limited either by electron transport (\( P_1 \)) or by ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco) activity (\( P_2 \)) and described by:

\[
P_1 = \frac{J}{4.5 C_i + 10.5 \Gamma} \quad P_2 = \frac{V_{\text{max}}}{C_i - \Gamma} \quad \frac{1}{1 + \frac{C_i}{C_i - \Gamma}}
\]

where \( J \) is the electron transport rate (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)), representing the effect of light on photosynthesis, \( V_{\text{max}} \) is the maximum carboxylation rate (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)), varying with leaf enzyme content which is regulated by both species characteristics and nutrient availability in ecosystems, \( C_i \) is the intercellular CO\(_2\) concentration (p.p.m.) and regulated by water status, \( \Gamma \) is the CO\(_2\) compensation point without dark respiration (p.p.m.) and related to temperature, and \( k \) is a coefficient (p.p.m.) and associated with enzyme kinetics and varies with species. By varying these parameters, the Farquhar et al. (1980) model captures essential features of environmental physiology of leaf photosynthesis.

Among all the parameters, the two parameters \( J \) and \( V_{\text{max}} \) are most variable (Wullschleger, 1993). Parameter \( V_{\text{max}} \) ranges from 6 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) for the coniferous species *Picea abies* to 194 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) for the agricultural species *Beta vulgaris* and averages 64 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) for 109 species. Parameter \( J \) increases with light in a rectangular–hyperbolic shape and reaches a maximum \( J_{\text{max}} \) (Farquhar et al., 1980). The latter also varies greatly among species (Wullschleger, 1993). High variability of the two parameters make it difficult to extrapolate leaf-level studies across scales.

To eliminate the parameters \( J \) and \( V_{\text{max}} \), Luo & Mooney (1995) defined a leaf-level factor (\( \mathcal{L}' \), p.p.m.\(^{-1} \)) as:

\[
\mathcal{L}' = \frac{P_2}{P_1} \quad \text{and} \quad \mathcal{L} = \frac{\mathcal{L}'}{C_i}
\]

where \( C_a \) is the atmospheric CO\(_2\) concentration. The \( \mathcal{L} \) factor denotes the relative leaf photosynthetic response to 1 p.p.m. \( C_a \) change. With an assumption that \( C_i \) is proportional to \( C_a \) as:

\[
C_i = \alpha C_a, \quad 0 < \alpha < 1
\]

the corresponding \( \mathcal{L} \) factor derived from Equation 1 is

\[
\mathcal{L}_1 = \frac{15 \alpha \Gamma}{(\alpha C_a - \Gamma)(4.5 \alpha C_a + 10.5 \Gamma)}
\]

\[
\mathcal{L}_2 = \frac{\alpha (K + \Gamma)}{(\alpha C_a - \Gamma)(\alpha C_a + K)}
\]

Parameters \( J \) and \( V_{\text{max}} \) are eliminated from eqn (4) because \( \mathcal{L}_1 \) and \( \mathcal{L}_2 \) are a measure of relative response. Eliminating \( J \) and \( V_{\text{max}} \) from the equation suggests that the \( \mathcal{L} \) factor is independent of the light and nutrient environment and species characteristics. The resultant \( \mathcal{L} \) factor is only a function of \( \alpha \), \( \Gamma \), \( K \), and \( C_a \). Sensitivity analysis indicates that variation in parameter \( \alpha \), \( \Gamma \), and \( K \) within range of the general growth environment leads to 15% or less changes in predicted values of the \( \mathcal{L} \) factor (Luo & Mooney, 1995). Thus, the \( \mathcal{L} \) factor is invariant but a function of \( C_a \).

Ecological difficulties in studying global phenomena lie in diverse species characteristics and environmental heterogeneity across different spatial and temporal scales. The traditional methods to overcome the difficulties are by dividing the earth system into less heterogeneous subunits, e.g. vegetation and soil types (Prentice & Fung, 1990; Melillo et al., 1993; Potter et al., 1993) or even individual plants (Smith et al., 1992). In that work, we also split the global photosynthetic carbon influx into the basic unit of the biochemical reaction of photosynthesis. Traditional approaches use empirical values as parameters to represent each subunit in the earth system, whereas the relative photosynthetic response to CO\(_2\) (the \( \mathcal{L} \) factor) is identified as an approximate constant for almost all C3 plants in the earth system that renders the extrapolation power to the \( \mathcal{L} \) factor.

Since the \( \mathcal{L} \) factor is derived simply from the Farquhar et al. (1980) model which predicts photosynthesis of virtually all C3 plants, the vast majority in global terrestrial ecosystems, the property of the \( \mathcal{L} \) factor, being an approximate constant but a function of \( C_a \), propagates to the majority of terrestrial plants in the earth system. Thus, the \( \mathcal{L} \) factor is able to estimate the additional amount of annual photosynthetic carbon influx (\( \Delta P_{\mathcal{G}} \), Gt yr\(^{-1} \)), stimulated by an increase in atmospheric CO\(_2\) concentration, as:

\[
\Delta P_{G,1} = \mathcal{L}_1 P_{G} \Delta C_a
\]

\[
\Delta P_{G,2} = \mathcal{L}_2 P_{G} \Delta C_a
\]

where $\Delta P_{C1}$ and $\Delta P_{C2}$ are the lower and upper limits of $\Delta P_C$, respectively, and $\Delta C_a$ is the annual change in atmospheric CO$_2$ concentration. At $C_a = 357$ p.p.m. in 1993, the lower and upper limits of $\Delta P_C$ are 0.21-0.45 Gt yr$^{-1}$, respectively, with $\Delta C_a = 1.5$ p.p.m. and $P_C = 120$ Gt yr$^{-1}$ (Olson, Watts & Allison, 1983).

When $\Delta C_a$ is sufficiently large, CO$_2$ stimulation of the global carbon influx cannot be estimated simply by eqn (5). Leaf acclimation and canopy adjustment induced by long-term growth in the CO$_2$-enriched environment could be significant enough to obscure the primary effect of the CO$_2$ increase on photosynthetic carbon influx. The biogeochemical cycle of nitrogen could be altered substantially by additional carbon input to regulate leaf and canopy photosynthetic properties. It is, therefore, imperative to understand adjustments in leaf properties, canopy structure and ecosystem nitrogen dynamics before we can possibly quantify long-term stimulation of the global carbon influx.

**ADJUSTMENTS IN LEAF PHOTOSYNTHETIC PROPERTIES**

It is a well-known phenomenon that photosynthetic responses to elevated CO$_2$ vary greatly among species and with growth conditions. Growth in 2 × current ambient CO$_2$ concentration leads to increased photosynthetic capacity for plant species *Solanum tuberosum* (Sage, Sharkey & Seemann, 1989) and *Glycine max* (Campbell, Allen & Bowes, 1988) and decreased photosynthetic capacity for *Brassica oleracea*, *Solanum melongena* (Sage et al., 1989), *Gossypium hirsutum* (Wong, 1990) and *Lolium perenne* (Ryle, Powell & Tewson, 1992b). It has been proposed that variable responses of photosynthesis to elevated CO$_2$ result from differential effects of CO$_2$ on biochemical and morphological processes (Luo, Field & Mooney, 1994), altering $J_{\text{max}}$ (the maximum $J$) and $V_{\text{max}}$. When $J$ and $V_{\text{max}}$ vary with CO$_2$ concentration, the $L'$ factor is modified as

$$L'_1 = L_1 + \frac{1}{J} \frac{dJ}{dC_a}$$

$$L'_2 = L_2 + \frac{1}{V_{\text{max}}} \frac{dV_{\text{max}}}{dC_a}$$

Eqn 6 indicates that if globally averaged $J$ and $V_{\text{max}}$ decrease by 10% in 700 p.p.m. CO$_2$ concentration in comparison to those in 350 p.p.m., the modified $L'$ factor ($L'$), on average, should be smaller by 0.000286 p.p.m.$^{-1}$ than $L$. It is translated into a difference of 0.0514 Gt yr$^{-1}$ between $\Delta P_{C1}$ and $\Delta P_{C2}$, where $\Delta P_C$ ranges from 0.057 to 0.21 Gt yr$^{-1}$ for the lower limit and from 0.17 to 0.46 Gt yr$^{-1}$ for the upper limit if $C_a$ increases 1.5 p.p.m. each year and $P_C = 120$ Gt yr$^{-1}$.

It will remain difficult to know how much globally averaged $J$ and $V_{\text{max}}$ change as atmospheric CO$_2$ concentration is gradually increasing. Based on a limited set of data, two recent reviews suggest that leaf photosynthetic capacity aggregated over a group of species changes little with CO$_2$ (Sage, 1994; Luo, 1995). From theoretical interpretations of about 40 A/C$_i$ (assimilation versus intercellular CO$_2$ concentration) curves, Sage (1994) concluded that growth in elevated CO$_2$ leads to higher photosynthetic capacity than in ambient CO$_2$ for twelve of twenty-seven species in pot studies and for two of three species in field studies. Luo (1995) used nitrogen–photosynthesis relationships (Harley et al., 1992) and predicted that $J_{\text{max}}$ and $V_{\text{max}}$ decreased by 1.7% for all thirty-three species surveyed from published papers and by 4.1% for a subgroup of eleven crop species, and by 1.1% for a subgroup of twenty-two wild species with a doubled CO$_2$ concentration (Table 1). Small regulation in photosynthetic capacity on average of a group of species suggests trivial adjustment of leaf properties on the global scale.

**ADJUSTMENTS IN CANOPY STRUCTURE**

One of the key determinants of carbon fixation by ecosystems is the amount of photosynthetic machinery per unit area of land. Although elevated CO$_2$ has been speculated to stimulate canopy development, leading to greater leaf area index (LAI), field data are scant. An experiment in artificial tropical ecosystems indicated that elevated CO$_2$ did not change canopy structure and LAI (Körner & Arnone, 1992). Experimental studies on ponderosa pines at Placerville, California, however, shows that elevated CO$_2$ changes canopy structure and leads to a greater LAI (J. T. Ball, pers. comm.).

Indirect measurements also suggest potential changes in foliar canopy in elevated CO$_2$ (Gunderson & Wullschleger, 1994). Elevated CO$_2$ will increase carbohydrate availability in leaves, leading to increased rate of leaf expansion and large leaf area per plant. Ontogeny of plants may be also accelerated in elevated CO$_2$, resulting in fast development of the canopy. Leaf area ratio (leaf weight per plant weight) may decrease but total leaf area usually increases. CO$_2$-induced changes in branching patterns also, potentially, affect canopy development. Because plants in elevated CO$_2$ are able to gain more carbon under low irradiances and keep more leaves in shade, elevated CO$_2$ may also lead to larger LAs in mature stands. These speculations, however, still need to be tested in the field. If growth in elevated CO$_2$ leads to higher leaf area in the canopy, ecosystem photosynthetic capacity is expected to increase in elevated CO$_2$ (Long & Drake, 1991). With little data available, however, it is premature to evaluate any effect of canopy adjustments on global carbon influx.

<table>
<thead>
<tr>
<th>Group</th>
<th>Size</th>
<th>Photosynthetic capacity (elevated/ambient)</th>
</tr>
</thead>
<tbody>
<tr>
<td>All species</td>
<td>33</td>
<td>0.979 ± 0.104</td>
</tr>
<tr>
<td>Wild species</td>
<td>22</td>
<td>0.989 ± 0.098</td>
</tr>
<tr>
<td>Crop species</td>
<td>11</td>
<td>0.959 ± 0.117</td>
</tr>
</tbody>
</table>

TABLE 1. Variation (mean ± SD) in CO$_2$-induced changes in photosynthetic capacity among thirty-three species and the two subgroups of wild and crop species. Data are adopted from Luo (1995).
ADJUSTMENTS IN ECOSYSTEM NITROGEN AVAILABILITY

Nitrogen and carbon assimilation

Nitrogen availability in ecosystems could alter photosynthetic capacity per unit of leaf area (Field & Mooney, 1986), change leaf area expansion (Nijstaka, 1990) and modify canopy structure (Hirose, Werger & van Rhenen, 1989). Because of the close links between nitrogen and photosynthesis in ecosystems, it has been hypothesized that potential stimulation of photosynthesis by elevated CO2 would be regulated strongly by nitrogen supply. Pot studies indicate that most species have larger photosynthetic responses to elevated CO2 with nitrogen fertilization than without fertilization (Gunderson & Wulfschleger, 1994). However, no evidence of greater feedback inhibition at lower N supply was found for Chenopodium album (Sage, 1994).

Leaf area expansion is greater in elevated CO2 than ambient CO2 and in high nitrogen than in low nitrogen. Percentage increases in leaf area expansion in elevated CO2, however, only sightly increased with nitrogen for Gossypium hirsutum (Wong, 1979). In contrast, total leaf area increased by 20% for Giliricidia sepium with nitrogen fertilization and was unchanged without fertilization in elevated CO2 compared with that in ambient CO2 (Thomas et al., 1991). For a whole plant, net assimilation rate of wheat was substantially higher in elevated than in ambient CO2 but the CO2 stimulation of carbon assimilation was not influenced by nitrogen supply (Hocking & Meyer, 1991; Fig. 1). Evaluation of interactive effects of CO2 and nitrogen on canopy development is important but requires more field studies. Nonetheless, ecosystem nitrogen availability is one of the important parameters which deserves careful examination.

Nitrogen availability in ecosystems

Nitrogen which is readily available for plants to take up is NH4 and NO3 in the labile pool. The amount of nitrogen in the labile pool is determined by a balance of several fluxes, including plant uptake, mineralization of soil organic nitrogen, immobilization of labile nitrogen, nitrogen deposition, fixation and denitrification, volatilization and leaching (Fig. 2). Pumping more carbon into terrestrial ecosystems in the CO2-enriched environment may alter directly plant uptake, fixation and mineralization/immobilization, leading to changes in ecosystem nitrogen dynamics.

Elevated CO2 generally stimulates plant biomass growth, demanding more nitrogen supply from soils. Total nitrogen uptake, for example, increased by 110.4% for Eucalyptus grandis (Conroy, Milham & Barlow, 1992) and by 99.9% for Trifolium repens (Ryle, Powell & Davidson, 1992a) when plants grew in elevated CO2 compared with plants grown in ambient CO2. Increased demand in nitrogen uptake is partially offset by an increase in plant nitrogen use efficiency (NUE). Biomass growth, for instance, increases by 26.2% for Abutilon theophrasti in elevated CO2 whereas nitrogen content in the plants only increased by 7.4% because of an 17.5% increase in NUE (Coleman & Bazzaz,

![FIG. 1. Net assimilation rate of Triticum aestivum at two CO2 and five nitrogen levels. Elevated CO2 significantly increased net assimilation rate. The CO2 stimulation of assimilation rate did not change much with nitrogen. Data are from Hocking & Meyer (1991).](image)

![FIG. 2. Schematic illustration of soil nitrogen dynamics, focusing on changes of labile nitrogen as influenced by an increase in atmospheric CO2 concentration and nitrogen deposition. In elevated CO2, plants demand more nitrogen supply to match enhanced biomass growth, leading to increased plant nitrogen uptake. Elevated CO2 also increases carbon release to rhizosphere, altering nitrogen mineralization/immobilization. Symbolic and free-living microbial fixation of nitrogen may be crucial in determining ecosystem nitrogen availability long term. Aerial nitrogen deposition adds a large amount of nitrogen into terrestrial ecosystems at the global scale. Denitrification, volatilization and leaching may also be changed.](image)
Elevated CO₂ increases total plant biomass by 50.8% ± 64.2% (mean ± standard deviation, n = 58) and increases total plant nitrogen content by 6.4% ± 30.9%. The non-proportional increase in total plant nitrogen content compared with the increase in total biomass results from increased nitrogen use efficiency and substantially reduces nitrogen demand in elevated CO₂. Date are from studies on species Abutilon theophrasti (Coleman & Bazzaz 1992), Agoseris capillaris (Williams, Garbutt & Bazzaz, 1988), Amaranthus retroflexus (Coleman & Bazzaz, 1992), Betula nana (Oberbauer et al., 1986), Carex bigelowii (Oberbauer et al., 1986), Castanea sativa (Mousseau & Enoch, 1989), Eichhornia crassipes (Spencer & Boves, 1986), Eucalyptus grandis (Conroy et al., 1992), Gliricidia sepium (Thomas et al., 1991), Glycine max (Cure, Israel & Rusby, 1988), Gossypium hirsutum (Wong, 1979), Lasthenia glutinosa, Leyia platyglossa (Williams et al., 1988), Ledum palustre (Oberbauer et al., 1986), Lolium perenne (Ryle et al., 1992b), Medicago sativa (MacDowall, 1982), Micropus Californicus, Microseris sp., Plantago erecta (Williams et al., 1988), Quercus alba (Norbay, O’Neill & Luxmoore, 1986), Salix myrsinifolia (Julkunen-Titto, Tahvanainen & Silvola, 1993), Trifolium repens (Ryle et al., 1992a), Triticum aestivum (Hocking & Meyer, 1991) and Zea mays (Wong, 1979).}

In an average of fifty-eight studies, biomass growth increased by 50.8% in elevated CO₂ relative to that in ambient CO₂. The increase in biomass was much higher than nitrogen demand. The latter increased only by 6.4% in elevated CO₂ (Fig. 3). Even with increased NUE, intact ecosystem studies on ponderosa pines in Placerville, California indicated that increased soil exploration and nitrogen uptake were the major mechanisms by which the seedlings were able to respond to elevated CO₂ under N limitation (Johnson et al., 1995).

When additional carbon is translocated into soils in elevated CO₂, soil microbial populations and activities are altered as to influence nitrogen immobilization and mineralization. Körner & Arnone (1992) found that elevated CO₂ reduces soil carbon and increases soil respiration and nitrate leaching in an artificial tropical ecosystem. They attributed these responses to increased soil organic matter decomposition in the rhizosphere. Similarly, Zak et al. (1993) found increased microbial biomass, carbon and nitrogen mineralization in the rhizosphere soils. In contrast, a microcosm study indicated that soil microbial carbon and nitrogen were higher by about 40% in a tall herb community and by more than 80% in an acidic grassland in elevated CO₂ than in ambient CO₂ (Diaz et al., 1993). The authors suggested that elevated CO₂ causes an increase in carbon release into the rhizosphere, leading to mineral nutrient sequestration by the expanded microflora and a consequent nutritional limitation on plant growth. Johnson et al. (1995) found no change in nitrogen mineralization due to elevated CO₂ in a field study at Placerville, California.

Biological nitrogen fixation by symbiotic microorganisms, free-living bacteria and cyanobacteria has fixed most nitrogen in vegetation and soils. The energy supply driving this fixation is entirely from the oxidation of photosynthetically fixed carbohydrates. The amount of nitrogen available for mineralization within an ecosystem is determined by the availability of the reduced carbon energy sources from plants. Thus, as elevated CO₂ consistently increases the sugar and starch content of vegetation, it is likely that the nitrogen content in an ecosystem will increase to match the increased photosynthetic potential for the long term (Gifford, 1992; 1994).

Another source of nitrogen supply to terrestrial ecosystems is not directly related to an increase in atmospheric CO₂ concentration, but through nitrogen deposition. Schlesinger & Hartley (1992) estimate that wet and dry deposition of ammonia nitrogen on land is 40 Mt (Mega tons = 1012 g) N yr⁻¹. Deposition of other compound nitrogen is about 10–40 Mt N yr⁻¹ (Pearson & Stewart, 1993). The amount of nitrogen input through deposition into the terrestrial ecosystems could stimulate a large amount of global carbon uptake (Schindler & Bayley, 1993; Hudson, Gherini & Goldstein, 1994).

As elevated CO₂ alters plant uptake, mineralization, immobilization and fixation, the pool size of labile nitrogen in soils would consequently be changed, potentially leading to changes in rates of denitrification, volatilization and leaching. Indeed, elevated CO₂ increased nitrate leaching in an artificial tropical ecosystem, resulting from increased decomposition (Körner & Arnone, 1992). No data are available to evaluate CO₂ effects on the other two processes.

**Integrative studies with models**

Nitrogen dynamics in ecosystems are highly complicated and involved with many processes and feedbacks. To investigate CO₂ effects on ecosystem nitrogen dynamics and their feedback effects on photosynthetic carbon uptake, we need to develop comprehensive models. Comins & McMurtrie (1993) integrated biogeochemical feedback of nitrogen into an ecosystem model. Although the model was not particularly developed for predicting effects of nitrogen feedback on photosynthesis, growth prediction could illustrate principles involved in photosynthesis. The model predicted that growth could increase by 27% in 700 p.p.m. CO₂ concentration in comparison with that at 350 p.p.m.
if nutrient supply is not limited. When the increase in photosynthetic carbon uptake at elevated CO₂ can not be matched by increases in nutrient supply, CO₂ stimulation of growth is only by 5%. The result was reached with an assumption that the stoichiometrical relationship between carbon and nitrogen is fixed in the biogeochemical cycles. In elevated CO₂ carbon becomes relatively abundant and nutrients scarce. Such a shift in carbon and nitrogen balance induces a suite of changes in ecosystems, including increased nitrogen use efficiency (Fig. 3) and changed carbon and nitrogen partitioning. Integrating various adjustments in plants and soils into the Comins & McMurtrie’s (1993) model, Kirschbaum et al. (1994) reported that elevated CO₂ could stimulate nearly 20% more growth.

In summary, using the δ factor to estimate the global photosynthetic carbon influx into the terrestrial ecosystems is valid only when the increase in atmospheric CO₂ concentration is small. When the increase is large, secondary effects of increased carbon supply on leaf growth, canopy development and ecosystem nitrogen availability may influence photosynthetic carbon influx substantially. Leaf-level adjustments have been investigated for years, whereas data on canopy and nitrogen adjustments are very scant. It appears that field ecosystem studies together with modelling exploration on canopy structure and nutrient dynamics in elevated CO₂ are urgently needed for our understanding of the global carbon influx over a long term with a large increase in atmospheric CO₂ concentration.

REFERENCES


