Long-term CO$_2$ stimulation of carbon influx into global terrestrial ecosystems: issues and approaches

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Abstract. Estimating the additional amount of global photosynthetic carbon influx into terrestrial ecosystems (P_G) becomes possible with a leaf-level factor ($\mathscr{L}$) developed by Luo & Mooney only when an increase in atmospheric CO$_2$ concentration (C_a) is small. Applying the $\mathscr{L}$ factor to study long-term stimulation of P_G with a large increase in C_a 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 CO$_2$ 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 CO$_2$ is largely unknown whereas indirect measurements suggest faster development of foliar canopy in elevated than ambient CO$_2$. Biogeochemical feedback of nitrogen on global carbon influx is involved with two general issues: CO$_2$ effects on ecosystem nitrogen availability and interactive effects of nitrogen and CO$_2$ on photosynthesis. Although nitrogen itself strongly influences photosynthesis, regulation of CO$_2$ 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 CO$_2$ stimulates more plant biomass growth, demanding more nitrogen uptake. Mineralization increased in two studies, decreased in one and was unchanged in one. CO$_2$ 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 CO$_2$ 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 CO$_2$ concentration is rapidly and unambiguously increasing (Siegenthaler & Sarmiento, 1993; Thorning, 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 C_a 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 CO$_2$ 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 (P_G) stimulated by a small increase in atmospheric CO$_2$ concentration (C_a) becomes possible with a leaf-level factor [$\mathscr{L} = dP/(P\,dC_a)$, where P is leaf photosynthesis] (Luo & Mooney, 1995). Although photosynthetic response to a C_a change (dP/dC_a) greatly varies with the light, water, nutrient environment and species characteristics, normalization of dP/dC_a against P eliminates their effects, leading to the $\mathscr{L}$ factor being an approximate constant at a given C_a. Thus, the $\mathscr{L}$ factor can cut across spatial scales to estimate the global photosynthetic carbon influx when a change in C_a is small enough.

Applying the $\mathscr{L}$ factor to study long-term stimulation of P_G by a large increase in C_a needs understanding of poss-

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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 $\mathscr{L}$ 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 $\mathscr{L}$ FACTOR

The $\mathscr{L}$ 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 $\mathscr{L}$ 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:

$$P_1 = J\frac{C_t - \Gamma}{4.5C_t + 10.5\Gamma}$$

$$\tag{1}$$

$$P_2 = V_{cmax}\frac{C_t - \Gamma}{C_t + k}$$

where J is the electron transport rate (μmol m^{-2} s^{-1}), representing the effect of light on photosynthesis, V_{cmax} is the maximum carboxylation rate (μmol m^{-2} s^{-1}), varying with leaf enzyme content which is regulated by both species characteristics and nutrient availability in ecosystems, C_t is the intercellular CO_2 concentration (p.p.m.) and regulated by water status, Γ 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_{cmax} are most variable (Wullschleger, 1993). Parameter V_{cmax} ranges from 6 μmol m^{-2} s^{-1} for the coniferous species *Picea abies* to 194 μmol m^{-2} s^{-1} for the agricultural species *Beta vulgaris* and averages 64 μmol m^{-2} s^{-1} for 109 species. 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). High variability of the two parameters make it difficult to extrapolate leaf-level studies across scales.

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

$$\mathscr{L} = \frac{1}{P}\frac{dP}{dC_a} \tag{2}$$

where C_a is the atmospheric CO_2 concentration. The $\mathscr{L}$ factor denotes the relative leaf photosynthetic response to 1 p.p.m. C_a change. With an assumption that C_t is proportional to C_a as:

$$C_t = \alpha \cdot C_a, \quad 0 < \alpha < 1 \tag{3}$$

the corresponding $\mathscr{L}$ factor derived from Equation 1 is

$$\mathscr{L}_1 = \frac{15\alpha\Gamma}{(\alpha C_a - \Gamma)(4.5\alpha C_a + 10.5\Gamma)}$$

$$\tag{4}$$

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

Parameters J and V_{cmax} are eliminated from eqn (4) because $\mathscr{L}_1$ and $\mathscr{L}_2$ are a measure of relative response. Eliminating J and V_{cmax} from the equation suggests that the $\mathscr{L}$ factor is independent of the light and nutrient environment and species characteristics. The resultant $\mathscr{L}$ factor is only a function of α, Γ, K, and C_a. Sensitivity analysis indicates that variation in parameter α, Γ, and K within range of the general growth environment leads to 15% or less changes in predicted values of the $\mathscr{L}$ factor (Luo & Mooney, 1995). Thus, the $\mathscr{L}$ 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 $\mathscr{L}$ factor) is identified as an approximate constant for almost all C3 plants in the earth system that renders the extrapolation power to the $\mathscr{L}$ factor.

Since the $\mathscr{L}$ 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 $\mathscr{L}$ factor, being an approximate constant but a function of C_a, propagates to the majority of terrestrial plants in the earth system. Thus, the $\mathscr{L}$ factor is able to estimate the additional amount of annual photosynthetic carbon influx (ΔP_G, Gt yr^{-1}), stimulated by an increase in atmospheric CO_2 concentration, as:

$$\Delta P_{G,1} = \mathscr{L}_1 \cdot P_G \cdot \Delta C_a$$

$$\tag{5}$$

$$\Delta P_{G,2} = \mathscr{L}_2 \cdot P_G \cdot \Delta C_a$$

where $\Delta P_{G,1}$ and $\Delta P_{G,2}$ are the lower and upper limits of ΔP_G, respectively, and ΔC_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 ΔP_G are 0.21–0.45 Gt yr^{-1}, respectively, with $\Delta C_a = 1.5$ p.p.m. and $P_G = 120$ Gt yr^{-1} (Olson, Watts & Allison, 1983).

When ΔC_a is sufficiently large, CO_2 stimulation of the global carbon influx can not 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 $2 \times$ 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_{max} (the maximum J) and V_{cmax}.

When J and V_{cmax} vary with CO_2 concentration, the $\mathcal{L}$ factor is modified as

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

$$\mathcal{L}'_2 = \mathcal{L}_2 + \frac{1}{V_{cmax}}\frac{dV_{cmax}}{dC_a}$$

$$(6)$$

Eqn 6 indicates that if globally averaged J and V_{cmax} decrease by 10% in 700 p.p.m. CO_2 concentration in comparison to those in 350 p.p.m., the modified $\mathcal{L}$ factor ($\mathcal{L}'$), on average, should be smaller by 0.000286 p.p.m.$^{-1}$ than $\mathcal{L}$. It is translated into a difference of 0.0514 Gt yr^{-1} between $\Delta P_G'$ and ΔP_G, where ΔP_G 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 $P_G = 120$ Gt yr^{-1}.

It will remain difficult to know how much globally averaged J and V_{cmax} 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 intercellu-

lar 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_{max} and V_{cmax} 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 LAIs 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 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).

Group	Size	Photosynthetic capacity (elevated/ambient)
All species	33	0.979 ± 0.104
Wild species	22	0.989 ± 0.098
Crop species	11	0.959 ± 0.117

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 (Nijkstra, 1990) and modify canopy structure (Hirose, Werger & van Rheenen, 1989). Because of the close links between nitrogen and photosynthesis in ecosystems, it has been hypothesized that potential stimulation of photosynthesis by elevated CO_2 would be regulated strongly by nitrogen supply. Pot studies indicate that most species have larger photosynthetic responses to elevated CO_2 with nitrogen fertilization than without fertilization (Gunderson & Wullschleger, 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 CO_2 than ambient CO_2 and in high nitrogen than in low nitrogen. Percentage increases in leaf area expansion in elevated CO_2, however, only sightly increased with nitrogen for *Gossypium hirsutum* (Wong, 1979). In contrast, total leaf area increased by 20% for *Gliricidia sepium* with nitrogen fertilization and was unchanged without fertilization in elevated CO_2 compared with that in ambient CO_2 (Thomas *et al.*, 1991). For a whole plant, net assimilation rate of wheat was substantially higher in elevated than in ambient CO_2 but the CO_2 stimulation of carbon assimilation was not influenced by nitrogen supply (Hocking & Meyer, 1991; Fig. 1). Evaluation of interactive effects of CO_2 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 NH_4^+ and NO_3^- 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 CO_2-enriched environment may alter directly plant uptake, fixation and mineralization/immobilization, leading to changes in ecosystem nitrogen dynamics.

Elevated CO_2 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 CO_2 compared with plants grown in ambient CO_2. Increased demand in nitrogen uptake is partially offset by an increase in plant nitrogen use efficiency (NUE). Biomass growth, for instance, increases
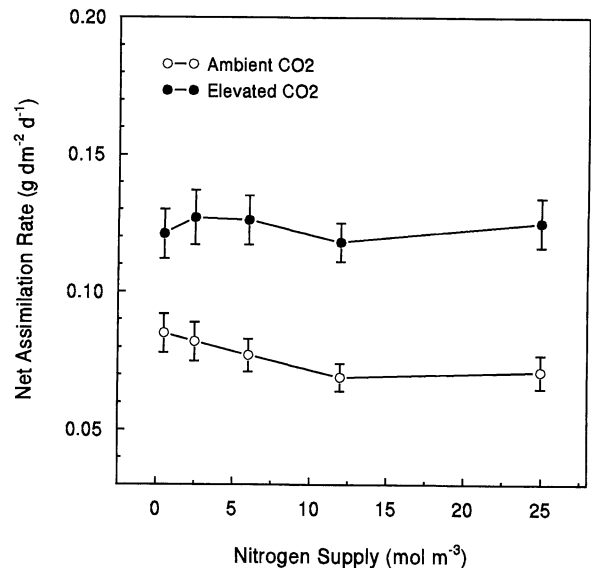

FIG. 1. Net assimilation rate of *Triticum aestivum* at two CO_2 and five nitrogen levels. Elevated CO_2 significantly increased net assimilation rate. The CO_2 stimulation of assimilation rate did not change much with nitrogen. Data are from Hocking & Meyer (1991).

by 26.2% for *Abutilon theophrasti* in elevated CO_2 whereas nitrogen content in the plants only increased by 7.4% because of an 17.5% increase in NUE (Coleman & Bazzaz,
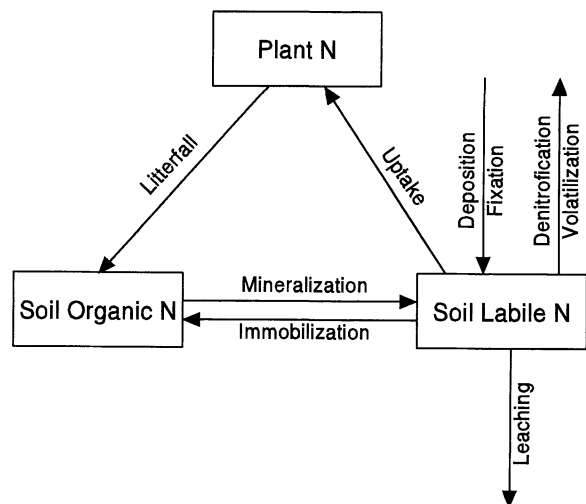

FIG. 2. Schematic illustration of soil nitrogen dynamics, focusing on changes of labile nitrogen as influenced by an increase in atmospheric CO_2 concentration and nitrogen deposition. In elevated CO_2, plants demand more nitrogen supply to match enhanced biomass growth, leading to increased plant nitrogen uptake. Elevated CO_2 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.
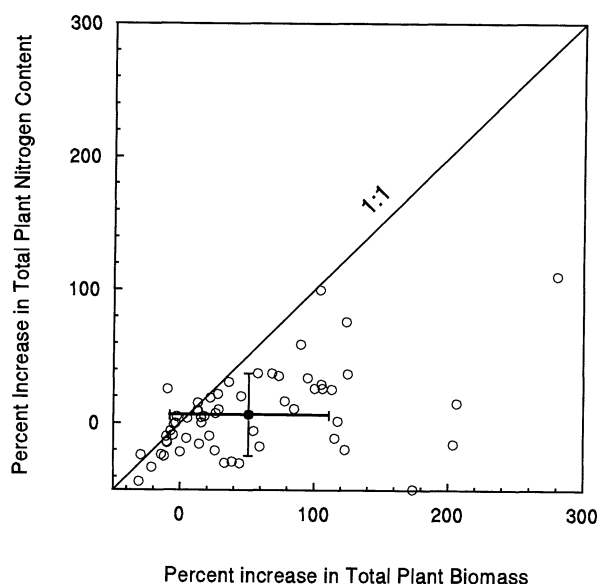
FIG. 3. Elevated CO_2 increases total plant biomass by 50.8% ± 64.2% (mean ± standard deviation, $n = 58$) and increases total plant nitrogen content by 6.4% ± 30.9%. The non-proportional increase in total plant nitrogen content compared with the increase in total biomass results from increased nitrogen use efficiency and substantially reduces nitrogen demand in elevated CO_2. 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), *Calluna vulgaris* (Woodin *et al.*, 1992), *Carex bigelowii* (Oberbauer *et al.*, 1986), *Castanea sativa* (Mousseau & Enoch, 1989), *Eichhornia crassipes* (Spencer & Bowes, 1986), *Eucalyptus grandis* (Conroy *et al.*, 1992), *Gliricidia sepium* (Thomas *et al.*, 1991), *Glycine max* (Cure, Israel & Rufty, 1988), *Gossypium hirsutum* (Wong, 1979), *Lasthenia glabrata, Layia 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* (Norby, 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).

1992). In an average of fifty-eight studies, biomass growth increased by 50.8% in elevated CO_2 relative to that in ambient CO_2. The increase in biomass was much higher than nitrogen demand. The latter increased only by 6.4% in elevated CO_2 (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 CO_2 under N limitation (Johnson *et al.*, 1995).

When additional carbon is translocated into soils in elevated CO_2, soil microbial populations and activities are altered as to influence nitrogen immobilization and mineralization. Körner & Arnone (1992) found that elevated CO_2 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 CO_2 than in ambient CO_2 (Diaz *et al.*, 1993). The authors suggested that elevated CO_2 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 CO_2 in a field study at Placerville, California.

Biological nitrogen fixation by symbiotic micro-organisms, 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 CO_2 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 CO_2 concentration, but through nitrogen deposition. Schlesinger & Hartley (1992) estimate that wet and dry deposition of ammonia nitrogen on land is 40 Mt (Mega tons $= 10^{12}$ 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 CO_2 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 CO_2 increased nitrate leaching in an artificial tropical ecosystem, resulting from increased decomposition (Korner & Arnone, 1992). No data are available to evaluate CO_2 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 CO_2 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. CO_2 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 CO_2 can not be matched by increases in nutrient supply, CO_2 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 CO_2, 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 CO_2 could stimulate nearly 20% more growth.

In summary, using the $\mathscr{L}$ factor to estimate the global photosynthetic carbon influx into the terrestrial ecosystems is valid only when the increase in atmospheric CO_2 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 has 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 CO_2 are urgently needed for our understanding of the global carbon influx over a long term with a large increase in atmospheric CO_2 concentration.

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