

Ecosystem Responses to Rising Atmospheric CO₂: Feedbacks through the Nitrogen Cycle

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I. Introduction

Rising atmospheric CO₂ could alter soil nitrogen (N) cycling, shaping the responses of many terrestrial ecosystems to elevated CO₂. Increased carbon input to soil through increased root growth, altered litter quality, and increased soil water content through decreased plant water use in elevated CO₂ can all affect soil N transformations and thus N availability to plants. Nitrogen limits net primary productivity (NPP) in many terrestrial ecosystems, so changes in N availability to plants will influence NPP in an elevated CO₂ environment. Furthermore, changes in NPP will alter carbon uptake by the terrestrial biosphere, and thus feed back to rising atmospheric CO₂. Elevated CO₂ could also influence the processes that regulate N inputs to and losses from ecosystems—N fixation, gaseous N losses (N₂, N₂O, NO_x), and N leaching. Such changes could alter ecosystem nitrogen stocks and thus nitrogen available to support NPP. Additionally, soil emissions of N₂O contribute to the greenhouse effect and stratospheric ozone destruction, and emissions of NO_x contribute to photochemical smog and acid rain. Thus, by altering soil nitrogen cycling, elevated CO₂ could cause other changes in atmospheric chemistry. Predicting these feedbacks requires that we understand what changes in soil nitrogen cycling caused by elevated CO₂ are likely, as well as how such changes might vary among terrestrial ecosystems. Here, I discuss the mechanisms through which elevated CO₂ can cause changes in soil nitrogen cycling, and review what changes have been observed and what mechanisms implicated in studies to date.

II. Soil Nitrogen Cycle

The soil nitrogen cycle comprises plant, microbial, and abiotic nitrogen transformations (Fig. 1A). Nitrogen mineralization converts organic nitrogen to ammonium, making it available for uptake by plants, immobilization by microbes, nitrification, and volatilization as ammonia. In most terrestrial ecosystems, ammonium and nitrate are the dominant forms of nitrogen that plants take up, so mineralization is an important bottleneck regulating nitrogen availability to plants (Chapin, 1995). Some plants acquire much of their nitrogen through associations with nitrogen-fixing bacteria (which convert atmospheric N_2 to organic nitrogen) or through uptake of dissolved organic nitrogen. Both of these processes “short circuit” the mineralization bottleneck (Chapin *et al.*, 1993), adding qualitatively different control points to the nitrogen cycle (Eviner and Chapin, 1997). A common view holds that the balance of mineralization and NH_4^+ immobilization determines how much NH_4^+ is left over for plant NH_4^+ uptake and nitrification (Rosswall, 1982; Tiedje *et al.*, 1981; Myrold and Tiedje, 1986). However, some recent results show that plant NH_4^+ uptake can limit microbial immobilization (Norton and Firestone, 1996), and that nitrifiers may not be restricted to heterotrophic leftovers (Davidson *et al.*, 1990). Nitrification (the autotrophic oxidation of ammonia to nitrate) is the major biological nitrogen transformation controlling ecosystem losses of nitrogen because it produces N_2O and NO_x , and also provides substrate for denitrification (conversion of nitrate to N_2 , N_2O , and some NO_x) and for nitrate leaching.

III. Mechanisms through Which Elevated CO_2 Alters Soil Nitrogen Cycling

The responses of plants to elevated CO_2 provide the starting point for considering potential changes in soil nitrogen cycling. First, elevated CO_2 usually increases photosynthesis, often increasing plant growth. To the extent that greater plant growth increases their demand for belowground resources, carbon allocation to roots may increase (Rogers *et al.*, 1994). Increased root allocation can be manifested as increased standing root mass, but also as increased root turnover, respiration, and exudation (Norby, 1994; Day *et al.*, 1996; Cardon, 1996; Berntson and Bazzaz, 1996a), in all cases enhancing the flux of carbon from plants to soil (Van Veen *et al.*, 1991; van de Geijn *et al.*, 1993; Gorissen, 1996; Hungate *et al.*, 1997b). Greater availability of carbon to soil microorganisms is likely to alter soil nitrogen transformations (Fig. 1B).

Second, elevated CO_2 often decreases stomatal conductance and plant transpiration (Morrison, 1987). In ecosystems where plant canopies strongly

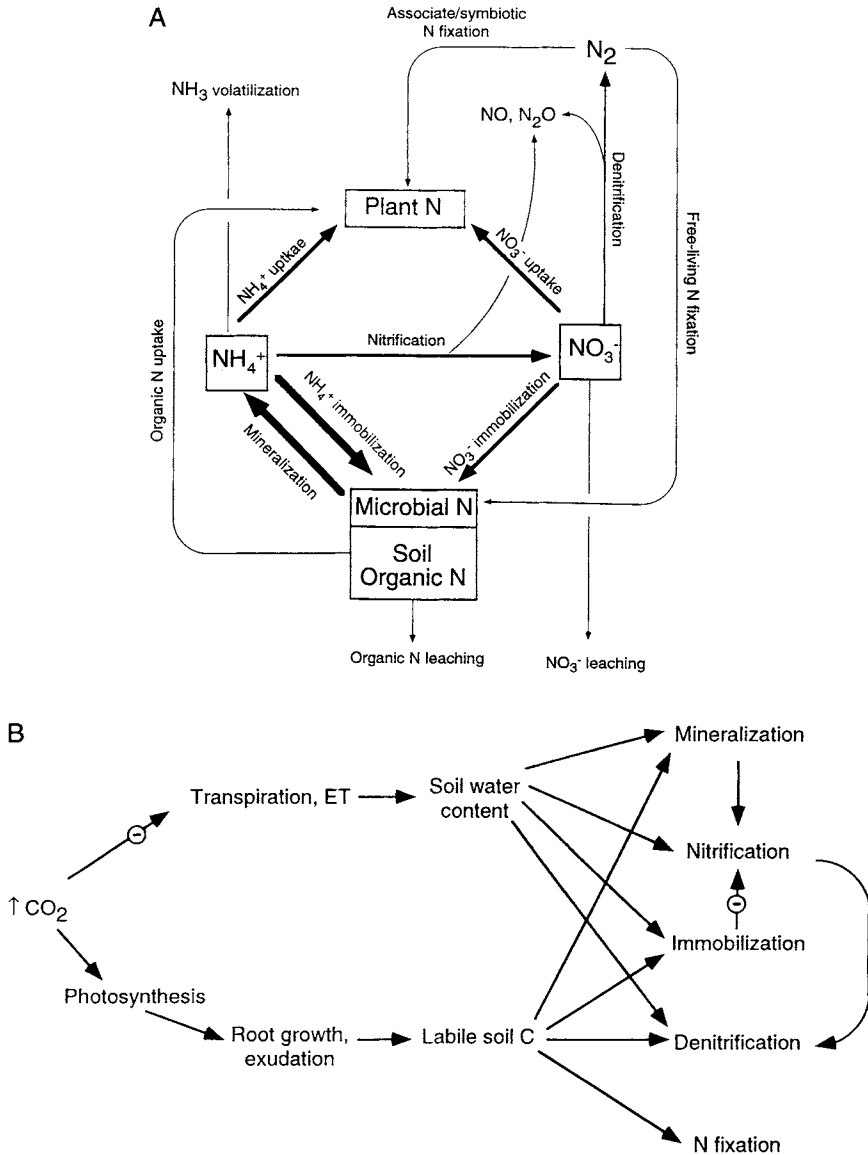


Figure 1 (A) Major nitrogen transformations in terrestrial ecosystems. Boxes show pools of nitrogen in the plant–soil system; arrows show fluxes between these pools and exchange with the atmosphere and groundwater. The magnitude of the flux is proportional to the thickness of the arrow. (B) Mechanisms through which increased carbon input to soil and increased soil water content alter microbial nitrogen transformations. Arrows marked with a minus indicate a negative effect; unmarked arrows indicate a positive effect.

influence evapotranspiration, reduced plant transpiration in elevated CO₂ can increase soil water content (Morgan *et al.*, 1994; Fredeen *et al.*, 1997; Hungate *et al.*, 1997a; Lutze, 1996; Bremer *et al.*, 1996), as long as there is no compensatory increase in leaf area (Field *et al.*, 1995). It is also possible that CO₂-induced increases in leaf area could more than compensate for lower transpiration per unit leaf area, resulting in greater ET in elevated CO₂, and thus drier soils. Changes in soil water content could alter soil nitrogen transformations in many ecosystems (Fig. 1B).

Third, elevated CO₂ usually decreases the nitrogen concentration of plant tissues, especially leaves, apparently due to reduced concentrations of Rubisco and other enzymes, as well as to greater accumulation of starch and other carbon storage compounds (Drake *et al.*, 1997). Reduced nitrogen concentrations in live plant tissue can lead to an increased litter carbon:nitrogen ratio (e.g., Cortrufo *et al.*, 1994), but apparently nitrogen retranslocation and carbon metabolism during senescence often eliminate the CO₂ effect on C:N (O'Neill and Norby, 1996; Canadell *et al.*, 1996; Hirschel *et al.*, 1997). This mechanism through which elevated CO₂ could alter soil nitrogen cycling has received considerable attention and is not discussed in detail here.

IV. Nitrogen Mineralization and Immobilization and Increased Carbon Input to Soil

The balance of nitrogen mineralization and immobilization depends on the carbon and nitrogen contents of microbial substrates. When carbon content is relatively high, immobilization will dominate and, conversely, when nitrogen content is relatively high, mineralization will dominate. Thus, the simplest prediction of the consequences of increased carbon input to soil is increased N immobilization by soil microorganisms. However, carbon input to soil can stimulate nitrogen mineralization. A burst of bacterial and fungal growth (caused by increased carbon availability) followed by protozoan and nematode grazing can cause nitrogen mineralization, because the nitrogen content of bacteria and fungi is relatively high compared to the nitrogen demand of their protozoan and nematode predators (Clarholm, 1985; Ingham *et al.*, 1985). The mineralization associated with the consumption of bacteria and fungi will be larger than the immobilization associated with their initial growth if the net effect of increased carbon input to soil was to transfer some of the total amount of organic nitrogen held in the total microbial N pool to the soil ammonium pool, or if the increase in carbon input to soil enhanced bacterial and fungal access to other sources of organic nitrogen (i.e., the "priming effect"). Although several studies have demonstrated that the "priming effect" oc-

curs (Clarholm, 1985, 1989; Helal and Sauerbeck, 1986), its quantitative significance may be negligible (Griffiths and Robinson, 1992). Understanding which pool(s) of soil organic nitrogen are susceptible to release via priming should assume a high priority for future research.

Lambourgh *et al.* (1983) and Luxmoore (1981) predicted that increased carbon input to soil in elevated CO₂ would alter the balance of nitrogen mineralization and immobilization, but Lambourgh (1983) predicted a relatively stronger increase in mineralization, while Luxmoore (1981) predicted a larger stimulation of immobilization. The two earliest tests of these ideas came to opposite conclusions, thus providing empirical support for both. In these experiments, elevated CO₂ stimulated root growth, thereby increasing the pool of carbon in the soil microbial biomass in poplar monocultures (Zak *et al.*, 1993) and in grass and herb communities (Díaz *et al.*, 1993). In the poplar study, increased carbon input to soil stimulated net nitrogen mineralization (measured by laboratory incubations), presumably increasing nitrogen availability to plants (Zak *et al.*, 1993). In contrast, carbon input to soil enhanced nitrogen immobilization in the soil microbial biomass in the grass and herb communities, apparently decreasing nitrogen availability to plants (Díaz *et al.*, 1993).

Subsequent experiments have also yielded conflicting results (summarized in Table I), though none since Zak *et al.* (1993) has found direct evidence that increased carbon input to soil stimulates nitrogen mineralization via priming. Billès *et al.* (1993) and Rouhier *et al.* (1994, 1996) used ¹⁴CO₂ pulse labeling to investigate CO₂ effects on carbon flow and nitrogen pools in wheat and sweet chestnut. In both experiments, elevated CO₂ increased the flux of carbon from plant roots to soil. However, the effects of elevated CO₂ on plant and soil inorganic nitrogen in the two experiments were in direct opposition: In wheat (Billès *et al.*, 1993), elevated CO₂ increased the sum of plant and soil inorganic nitrogen, but in sweet chestnut (Rouhier *et al.*, 1994), elevated CO₂ decreased the sum of plant and soil inorganic nitrogen. In the wheat experiment, and in similar experiments where elevated CO₂ increases the total mass of plant nitrogen, because the stimulation of photosynthesis in elevated CO₂ may directly enhance root growth, and thereby increase the volume of soil mined for nitrogen (Berntson and Woodward, 1992), it is not possible to separate this direct effect of elevated CO₂ from an indirect effect on plant growth caused by increased mineralization. Indeed, the former is a simpler explanation than the priming effect for the observation that elevated CO₂ increases total plant nitrogen. Explicitly testing the effects of increased carbon input to soil on the balance of mineralization and immobilization requires measuring these processes directly, preferably *in situ* (Berntson and Bazzaz, 1996b).

Other experiments support the idea that carbon input to soil stimulates nitrogen immobilization, thereby decreasing nitrogen availability to plants.

Table 1 Summary of Studies Investigating Feedbacks to Plant Nitrogen Availability in Elevated CO₂^a

Reference	System	↑ C input?	↑ soil H ₂ O?	Δ N avail	Δ MBN	Δ Plant N
Diaz <i>et al.</i> (1993)	Grassland microcosms (GC)	✓	N.R.		↑	↓ ^b
Zak <i>et al.</i> (1993)	Poplar (OTC)	✓	N.R.	↑		
Billes <i>et al.</i> (1993)	Wheat (GC)	✓	N.R.	(↑)		↑
Rouhier <i>et al.</i> (1996)	Sweet chestnut (GC)	✓	N.R.	↓		↓
Morgan <i>et al.</i> (1994)	C ₄ grassland (GC)	✓	✓	↓		↓
Johnson <i>et al.</i> (1997)	Ponderosa pine (OTC)	✓	N.R.	↓		
Matamala (1997)	Salt marsh (OTC)	✓	0	↓		
Rice <i>et al.</i> (1994), Owensby <i>et al.</i> (1993)	C ₄ grassland (OTC)	✓	✓		↑	↑
Hungate <i>et al.</i> (1996a)	Serpentine annuals (OTC)	✓	0		↓ ↑	↓ ↑ ^c
Hungate <i>et al.</i> (1996b)	Annual grasslands (OTC)	✓	✓	↑	0	↑
Berntson and Bazzaz (1996)	Yellow birch, deciduous forest (GC)	✓	N.R.	↑	0	↑

^a ✓ Indicates empirical support that elevated CO₂ caused increased C input to soil (support includes increased root growth, increased microbial biomass carbon, as well as increased C flow according to ¹⁴C measurements), and that elevated CO₂ caused increased soil moisture. Arrows under "Δ N avail," "Δ MBN," and "Δ Plant N" indicate whether CO₂ decreased (↓), increased (↑), or caused no change (0) in nitrogen availability, microbial biomass nitrogen, and total plant nitrogen, respectively. Measures of nitrogen availability include mineralization rates (net or gross, *in situ* or laboratory assays) and extractable soil nitrogen. Microbial biomass nitrogen is included as a separate category, because changes in it do not necessarily indicate changes in nitrogen availability to plants. N.R., no response.

^b Plant shoots only.

^c Depended on plant species.

In monocultures of *Bouteloua gracilis*, a C₄ grass, elevated CO₂ increased root growth and VAM infection, indicating greater carbon input to soil, and resulting in less extractable soil nitrate and less total plant nitrogen uptake (Morgan *et al.*, 1994). Increased immobilization resulting from increased carbon input to soil could explain this reduction in nitrogen availability. Elevated CO₂ reduced extractable NH₄⁺ and NO₃⁻ in soils planted with ponderosa pine after 3 yr, apparently due to increased immobilization in the soil microbial biomass (Henderson and Johnson, 1996). After 10 yr of exposure to elevated CO₂, extractable ammonium in soil was consistently lower throughout the summer growing season in a C₃ salt marsh, perhaps due to increased microbial immobilization of ammonium (Matamala, 1997). In this case, however, total plant nitrogen pools were not significantly different between CO₂ treatments (Matamala, 1997).

In some cases, though elevated CO₂ increases nitrogen immobilization in the soil microbial biomass, plant nitrogen pools also increase. For example, in an unfertilized C₄ grassland exposed to elevated CO₂ for 3 yr, elevated CO₂ increased nitrogen in the soil microbial biomass by 8–9% (Rice *et al.*, 1994) and total nitrogen pools in plants by 24% (calculated from Owensby *et al.*, 1993). Similarly, in six annual grasses and forbs under conditions where nutrients strongly limited plant growth, CO₂-induced changes in microbial nitrogen pools were parallel to CO₂-induced changes in plant nitrogen pools (Hungate *et al.*, 1996). Parallel increases in plant and microbial nitrogen pools in these experiments could be explained by increased mineralization via the priming effect (Zak *et al.*, 1993), though increased root growth and thus mining of nitrogen in a larger volume of soil may be a simpler explanation (Berntson and Woodward, 1992).

Berntson and Bazzaz (1996b) investigated the effects of elevated CO₂ on soil nitrogen cycling in deciduous forest microcosms. In these experiments, elevated CO₂ decreased gross nitrogen mineralization as well as both plant and microbial ammonium uptake, measured during a 48-h period after 14 months of treatment. The decrease in plant ammonium uptake was relatively larger than the decrease in microbial ammonium uptake. Sustaining these altered rates of microbial ammonium production and consumption over longer periods would cause reduced ammonium availability to plants, first because less ammonium is produced (i.e., gross mineralization decreases), but also because as a fraction of mineralized (i.e., available) ammonium, microbes immobilized relatively more in elevated compared to ambient CO₂ in this experiment. A reduction in the carbon quality of root-derived substrates could decrease both mineralization and immobilization (Berntson and Bazzaz, 1996b). Alternatively, decreased nitrogen cycling rates in this experiment could indicate a shift in the seasonal pattern of belowground activity under elevated CO₂. If, for example, plants were phenologically more advanced in elevated compared to ambient CO₂, and

if in this more advanced stage of growth they allocated less carbon to roots and more to aboveground sinks, this could explain the reduced plant ammonium uptake. Reduced carbon allocation to roots would also slow the carbon input that stimulates microbial growth, and thus production and consumption of ammonium.

Several possible reasons could account for this wide range of results. First, the methods for determining nitrogen availability differ in these experiments, ranging from instantaneous availability of inorganic nitrogen measured by soil extractions, to rates of mineralization and immobilization measured over 1 or 2 d, to the net balance of mineralization and immobilization measured by the amount of nitrogen in the soil microbial biomass, to the size of the potentially mineralizable pool of soil nitrogen. It is likely that some of the variation among these studies is due to differences in methodology. For example, if elevated CO_2 stimulated nitrogen immobilization *in situ*, thereby increasing the size of the microbial nitrogen pool, one might expect a laboratory incubation to show increased nitrogen mineralization (Zak *et al.*, 1993), because nitrogen sequestered in the microbial biomass *in situ* is released once cut off from a continual supply of root-derived carbon.

Second, the timescales of the experiments differ, ranging from several weeks to several years. Even in systems where the responses of the plant–soil system to elevated CO_2 are very similar, it is very likely that those responses change through time as the system “equilibrates” after the step change in atmospheric CO_2 concentration used in these experiments. For example, Berntson and Bazzaz (1997) found that elevated CO_2 decreased mineralization, ammonium immobilization, and plant ammonium uptake over a 48-h period after 14 months of growth. Despite this, elevated CO_2 increased the total mass of nitrogen in plants, an integrated measure of nitrogen uptake over the entire 14-month period. Thus, net feedbacks to the availability of nitrogen to plants strongly depended on the timescale at which the question was addressed. In this case, elevated CO_2 apparently stimulated nitrogen acquisition early in the experiment, but negative feedbacks to nitrogen availability through reduced mineralization eventually caused a decline in plant ammonium uptake, a pattern that, if sustained, could limit plant growth responses to elevated CO_2 .

Third, the plant species differ among these experiments. Plant responses to elevated CO_2 vary among plant species (Poorter, 1993), so it is not surprising that the effects of elevated CO_2 on soil nitrogen cycling might also vary among species. For example, the effects of elevated CO_2 on microbial nitrogen pools varied among six serpentine annuals, with some species showing increased and others decreased microbial nitrogen pools (Hungate *et al.*, 1996).

Finally, the effects of increased carbon input to soil on microbial nitrogen transformations may depend on the nutrient status of the soil. Just as litter decomposition depends on the relative availability of carbon and nutrients in the decomposing substrate (Melillo and Aber, 1982), the decomposition of soil organic matter in the rhizosphere may depend on soil nutrient status. Carbon sources in the rhizosphere vary simultaneously in carbon quality and nutrient content. Root-derived carbon substrates are lower in nitrogen content than older soil organic matter constituents, but root-derived carbon (excepting, perhaps, suberized cell walls) is more readily degraded (i.e., higher carbon quality) than older soil organic matter. Changes in nutrient availability can alter the relative rates at which microorganisms decompose these different carbon sources (Merckx *et al.*, 1987; Van Veen *et al.*, 1989; Liljeroth *et al.*, 1990), as described by the concept of "preferential substrate utilization" (Kuikman and Gorissen, 1993): Given adequate nutrient supply, microbes preferentially consume root-derived carbon (Van Veen *et al.*, 1989; Liljeroth *et al.*, 1990). If inorganic nutrients are scarce, root-derived carbon compounds accumulate in the soil as microbes preferentially degrade more nutrient-rich soil organic matter (Liljeroth *et al.*, 1990).

When some external factor (e.g., CO₂ concentration) stimulates root growth and causes greater input of root-derived carbon to the rhizosphere, changes in nitrogen availability to plants may thus depend on the nutrient status of the soil (Fig. 2). If nutrient availability is high, increased rhizodeposition in elevated CO₂ will drive nitrogen immobilization, because microbes preferentially consume the more labile root-derived carbon compounds and immobilize inorganic soil nitrogen to meet their nitrogen requirement. In this case, nitrogen availability to plants would decrease. If, on the other hand, nutrient availability is low, increased rhizodeposition may exacerbate microbial nutrient limitation. In this case, rhizodeposits may accumulate in the soil, causing little change in decomposition of soil organic matter; or, to the extent the priming effect occurs, increased rhizodeposition under strongly nutrient-limiting conditions may enhance microbial degradation of nutrient-rich soil organic matter. In this case, nitrogen availability to plants would increase.

Several experiments support the idea that decomposition in the rhizosphere in response to an increase in the supply of root-derived carbon depends on soil nutrient status. In wheat grown with high nitrogen supply, elevated CO₂ increased rhizodeposition, increased microbial use of rhizodeposits, and decreased decomposition of older soil organic matter (Lekkerkerk *et al.*, 1990; Kuikman *et al.*, 1991). Cardon (1996) also found that elevated CO₂ decreased decomposition of native soil organic matter, but only when soil nutrient availability was high. Under nutrient-limiting conditions, elevated CO₂ decreased microbial use of root-derived carbon

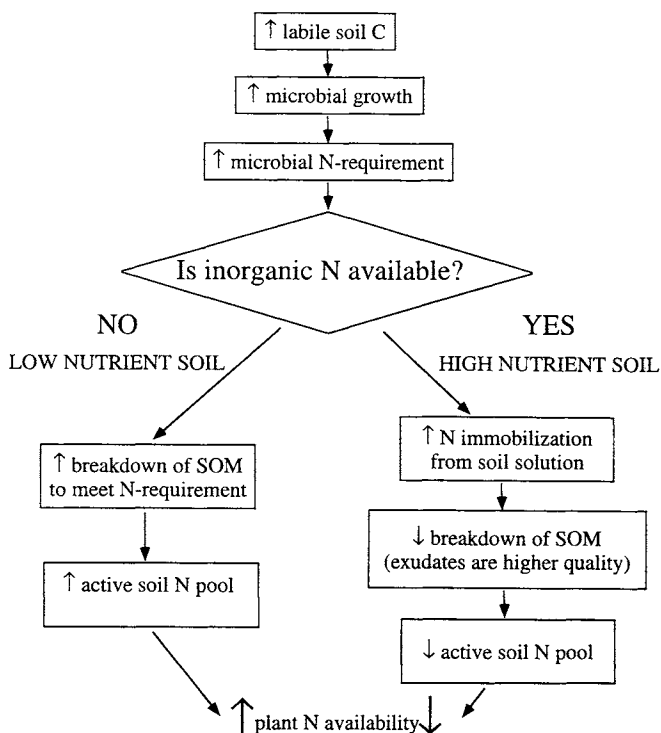


Figure 2 How soil nitrogen status may influence changes in nitrogen availability to plants that occur in response to increased carbon input to soil. See text for explanation.

compounds (Paterson *et al.*, 1996). In a recent experiment, however, elevated CO_2 had no effect on the decomposition of native soil organic matter at either low or high soil nutrient levels (van Ginkel *et al.*, 1996).

The nutrient dependence of decomposition in the rhizosphere may explain some of the variation in the direction of changes in nitrogen cycling observed in the studies cited. For example, Zak *et al.* (1993) grew their poplar trees in a "nutrient-poor soil," whereas Díaz *et al.* (1993) described their tall herb community as "high fertility." Given these albeit qualitative descriptions of soil nutrient status, the changes in nitrogen availability to plants observed in these studies match well the predictions of this framework.

V. Increased Carbon Flux to Soil and Nitrogen Inputs and Losses

Rates of transfer between organic and inorganic soil nitrogen pools (mineralization and immobilization) are the most important controls of

nitrogen availability to plants on the timescale of months to several years. As the timescale of inquiry expands to decades and centuries (the timescale of CO₂-induced global change), the processes that regulate ecosystem nitrogen inputs and losses—biological nitrogen fixation, atmospheric deposition, gaseous nitrogen emissions (N₂, N₂O, and NO_x), and nitrogen leaching—become increasingly important in determining nitrogen availability and nitrogen limitation of plant growth. In addition to altering nitrogen availability to plants in the short term, elevated CO₂ could also affect the processes that regulate nitrogen inputs to and losses from ecosystems. A greater supply of fixed carbon in elevated CO₂ can enhance nitrogen fixation by energy-limited nitrogen-fixing bacteria (Hardy and Havalka, 1976; Poorter, 1993; Soussana and Hartwig, 1996). Less often considered, elevated CO₂ could also affect nitrification and denitrification, the microbial nitrogen transformations that return mineral nitrogen to the atmosphere, as dinitrogen, nitrous oxide, or nitric oxide. Recent work in this area focuses on the idea that increased carbon input to soil is likely the major mechanism altering ecosystem nitrogen inputs and losses.

Several modeling studies show that small changes in annual rates of nitrogen inputs or losses can appreciably affect ecosystem carbon uptake over the timescale of centuries (Comins and McMurtrie, 1993; Gifford *et al.*, 1996). Thus, although very small changes in nitrogen inputs or losses would have negligible effects on the nitrogen budget in short-term CO₂ experiments, if such changes were sustained over several decades or centuries as CO₂ accumulates in the atmosphere, they could substantially affect ecosystem carbon cycling.

Empirical studies demonstrate that elevated CO₂ can also alter ecosystem nitrogen losses. By increasing labile carbon availability to carbon-limited denitrifiers, elevated CO₂ stimulated nitrogen losses through denitrification in the rhizosphere of wheat grown in hydroponic systems (Smart *et al.*, 1997). Similarly, elevated CO₂ enhanced nitrogen losses, presumably via denitrification, from soil planted with *Quercus agrifolia* seedlings (Hinkson, 1996). Though elevated CO₂ also increased asymbiotic nitrogen fixation in this study, the total mass of nitrogen in the system was lower in elevated CO₂, indicating that the stimulation of nitrogen losses was larger than the increase in nitrogen inputs (Hinkson, 1996). By contrast, in a C₃ salt marsh, elevated CO₂ decreased denitrification potential, possibly because increased labile carbon availability in elevated CO₂ enhanced nitrogen immobilization (Matamala, 1997), thereby limiting nitrate supply to denitrifiers.

In seasonally dry ecosystems, the first rains after a long drought stimulate microbial nitrogen transformations, including gaseous soil efflux of nitrous oxide and nitric oxide (Davidson, 1991). Such “wet-up” events can contribute substantially to the annual losses of nitrogen from seasonally dry ecosystems (Davidson, 1991). In a California annual grassland, elevated CO₂ increased root growth and the C:N ratio of root detritus after plant senes-

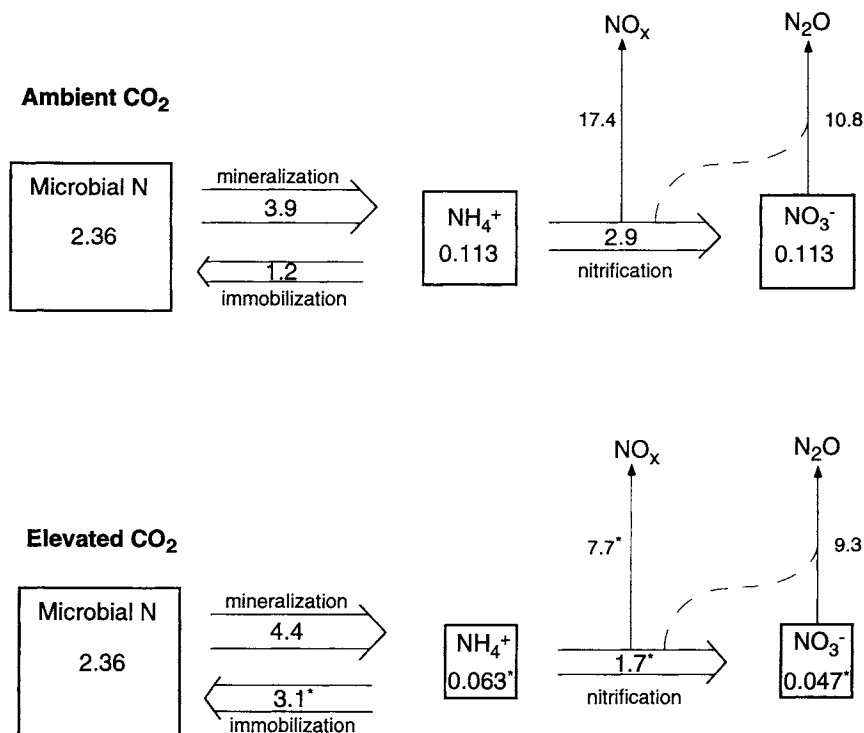


Figure 3 Nitrogen pools and fluxes under ambient and elevated CO₂ and nutrient-enriched soil during a 9-d period after the first autumn rains in a mediterranean annual grassland in California (data from Hungate *et al.*, 1997c). Plants were grown during the previous growing season under ambient and elevated CO₂, and high and low nutrients. Values for gross mineralization, immobilization, and nitrification are in g N m⁻² for the 9-d period. Values for net NO_x and N₂O flux are in mg N m⁻² 9d⁻¹. Values for microbial N are in gN m⁻² (at the end of the 9-d period), for ammonium and nitrate in g m⁻² (weighted average for the 9-d period). Values significantly affected by elevated CO₂ are indicated by an asterisk, * ($P < 0.05$).

cence (Hungate *et al.*, 1997c). At the end of the summer drought, this increase in root litter mass and C:N ratio stimulated nitrogen immobilization in the soil microbial biomass (Fig. 3). Under nutrient enrichment, higher immobilization decreased ammonium availability to nitrifiers, and thereby decreased nitrification and associated NO efflux from soil (Fig. 3). Total nitrogen losses due to NO efflux from soil were substantial in this experiment, so the reduction in NO efflux by elevated CO₂ could be quantitatively significant for nitrogen retention.

VI. Altered Nitrogen Cycling and Soil Water Content

Decreased plant transpiration in elevated CO₂ will increase soil moisture in ecosystems where plant transpiration is a large component of evapotranspiration, and if increases in soil evaporation, leaf area, or canopy temperature (Field *et al.*, 1995) do not offset reduced transpiration at the leaf level. Based on such considerations, Field *et al.* (1995) predicted that elevated CO₂ would increase soil water content in a broad range of grassland, shrubland, and forest ecosystems. Empirical work shows that elevated CO₂ increases soil water content in agricultural forb ecosystems (Clifford *et al.*, 1993) and in annual (Fredeen *et al.*, 1997; Field *et al.*, 1995) and perennial grasslands (Rice *et al.*, 1994; Ham *et al.*, 1995; Bremer *et al.*, 1996). Elevated CO₂ also increased soil water content in several grassland microcosm experiments (Lutze, 1996; Morgan *et al.*, 1994; Ross *et al.*, 1995).

Water content influences microbial nitrogen transformations in soil, so increased soil water content is another potentially important mechanism through which elevated CO₂ could alter soil nitrogen transformations. In two annual grassland ecosystems, elevated CO₂ increased gross nitrogen mineralization and plant nitrogen uptake (Hungate *et al.*, 1997c). Elevated CO₂ increased soil water content and labile carbon availability (measured as increased microbial biomass carbon) in this experiment, either of which could have been the mechanism increasing nitrogen mineralization. As discussed earlier, increased labile carbon availability could stimulate mineralization by increasing microbial growth, nitrogen uptake, and subsequent turnover of microbial cells (Zak *et al.*, 1993; Clarholm, 1985). Wetter soils could also enhance nitrogen mineralization by increasing substrate diffusion, by increasing motility of microorganisms, or by directly relieving physiological stress due to dry soils (Stark and Firestone, 1995). Thus, in this grassland experiment, there was evidence for two possible mechanisms that could have caused the observed increase in nitrogen mineralization. Soil water content was more strongly correlated to gross nitrogen mineralization than was microbial biomass carbon, suggesting that increased soil moisture was the more likely mechanism causing increased nitrogen mineralization (Hungate *et al.*, 1997a).

Rice *et al.* (1994) investigated the effects of elevated CO₂ on soil microbial respiration in a perennial C₄ grassland. In this experiment also, increased soil moisture may be the simplest explanation for increased microbial respiration in elevated CO₂ (Rice *et al.*, 1994). In this experiment, there was a strong correlation between the CO₂ effect on soil moisture and the CO₂ effect on microbial respiration over the 8-month period during which they were measured during both dry ($r = 0.74$) and wet ($r = 0.72$) years (Fig. 4). Total rainfall during these years was 669 cm in 1991 and 1028 cm

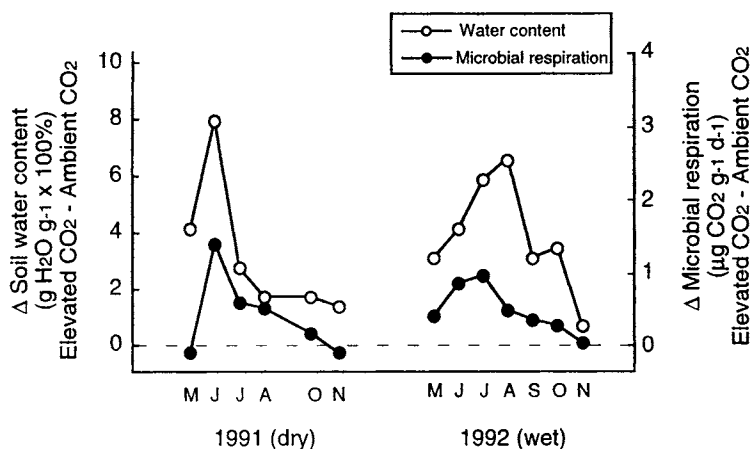


Figure 4 The relationship between the effects of elevated CO₂ on soil water content and on soil microbial respiration in an intact C₄ grassland for 2 yr (data replotted from Rice *et al.*, 1994). Values are the mean differences between the elevated and ambient CO₂ treatments in soil water content and microbial respiration rate. These absolute CO₂ effects on soil water content and microbial respiration rate are linearly correlated ($r^2 = 0.53$, $P = 0.005$).

in 1992, and mean soil water contents were 22.7 and 30.8%, respectively (Rice *et al.*, 1994). Despite these considerable differences in precipitation and soil moisture, the magnitude of the CO₂ stimulation of soil water content and of microbial respiration was comparable for the 2 yr, with water content increasing by 15 and 14% and microbial activity by 28 and 29% during 1991 and 1992, respectively (Fig. 4). Increased soil moisture in elevated CO₂ is a simple and plausible explanation for the observed increase in microbial respiration in this experiment given the strong correlation between CO₂ effects on soil moisture and soil microbial respiration and the known causal relationship between these in this grassland (Garcia, 1992).

VII. Relative Importance of Increased Carbon Input versus Altered Soil Water Content

The relative importance of the mechanisms through which elevated CO₂ alters nitrogen cycling will likely vary among ecosystems. Understanding this variation will aid in the effort to incorporate changes in soil processes in simulation models of the feedbacks of terrestrial ecosystem to rising CO₂. In part, such variation may involve a simple trade-off in which the magnitude of increased plant growth, and thus carbon input to soil, is

inversely related to the reduction in evapotranspiration (ET), and thus increased soil moisture. Elevated CO₂ is likely to cause the largest reductions in ET in ecosystems where aboveground growth responses to elevated CO₂ are smallest, for the simple reason that increased leaf area provides more transpiring surface, offsetting decreased transpiration per unit leaf area (Fig. 5). Thus, factors that favor large increases in aboveground growth in response to elevated CO₂ will limit reductions in ET, while factors that constrain aboveground growth responses to elevated CO₂ will allow reductions in ET. To the extent that aboveground growth is directly proportional to net ecosystem carbon uptake, the relative importance of feedbacks through increased carbon input to soil and altered soil moisture will have a simple, predictable relationship (Fig. 5).

For example, decreased evapotranspiration under elevated CO₂ is likely to be larger in a system dominated by C₄ plants than one dominated by C₃ plants, due to generally larger aboveground growth responses in C₃ plants (Poorter, 1993), whereas the stimulation of net ecosystem carbon uptake should be relatively stronger in C₃-dominated systems. Consistent with this, elevated CO₂ decreased evapotranspiration by 20% in a salt marsh dominated by C₃ plants and by 29% in one dominated by C₄ plants, whereas the stimulation of net ecosystem carbon uptake was larger in the C₃ marsh (56%) than in the C₄ marsh (24%) (Arp, 1991). Similarly, as growth and photosynthetic responses to CO₂ increase with nutrient availability (McGuire *et al.*, 1995) and temperature (Long and Drake, 1992), decreased

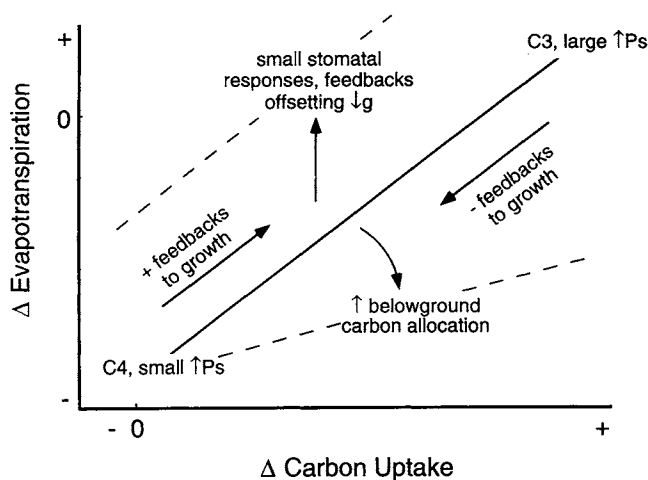


Figure 5 Predicted relationship between changes in soil water content and changes in carbon input to soil, based on a positive relationship between evapotranspiration and leaf area. See text for a discussion of this relationship, and of the factors that modify it.

ET in elevated CO_2 is likely to be more pronounced where low nutrient availability and low temperatures constrain aboveground plant growth responses to elevated CO_2 .

Several factors will modify this relationship. First, increased carbon allocation belowground allows greater carbon uptake with minimal increase in leaf area, weakening the trade-off between reduced ET and increased carbon input to soil (Fig. 5). Second, the CO_2 reduction in stomatal conductance is quite variable among species (Ellsworth *et al.*, 1995; Tissue and Oechel, 1987), apparently more variable than the stimulation of photosynthesis among C_3 species. Third, canopy roughness affects the translation of decreased conductance to decreased ET: In systems where the canopy is aerodynamically rough, CO_2 will have larger effects on ET than in systems where the canopy is aerodynamically smooth (Field *et al.*, 1995). In ecosystems dominated by species in which stomatal conductance is unresponsive to elevated CO_2 , or in systems where aerodynamically smooth canopies limit stomatal control of ET, the relationship between feedbacks through ET and through increased soil moisture will fall above the line shown in Fig. 5.

It is also likely that the relative importance of these feedbacks will change through time within ecosystems as they adjust to rising CO_2 concentrations (or to an experimental step change in CO_2). For example, if plant nitrogen acquisition increases as a result of increased nitrogen mineralization in wetter soils (Hungate *et al.*, 1997a), leaf area should increase, reducing the CO_2 effect on ET and limiting further increases in nitrogen cycling. On the other hand, if increased soil moisture enhances nitrogen losses or otherwise reduces nitrogen availability, this could reduce leaf area and amplify the CO_2 effect on ET, creating a strong negative feedback to increased plant growth in elevated CO_2 . For example, plant transpiration influences the height of the water table in coastal salt marshes and enhances sediment oxidation (Dacey and Howes, 1984). In these marshes, reduced ET in elevated CO_2 (Arp, 1991) could increase the height of the water table, thereby reducing sediment oxidation and associated nutrient mineralization. (Observing this phenomenon on the scale of a 1-m^2 plot would be difficult, because rapid lateral water flow in saturated soil would buffer any change in water table height over such a small area.) Similarly, a negative feedback to plant growth through nutrient accumulation in microbes and soil organic matter, by limiting increases in leaf area, would favor larger feedbacks through reduced ET.

VIII. Conclusions

Elevated CO_2 can alter soil nitrogen cycling by increasing carbon input to soil, a consequence of greater photosynthesis and increased belowground

allocation in response to elevated CO₂. Increased carbon input to soil in elevated CO₂ has been reported to increase, decrease, and have no effect on nitrogen availability to plants. Increased soil moisture is another important mechanism through which elevated CO₂ can alter nitrogen cycling in soil and N availability to plants, but the degree to which CO₂ increases soil moisture and the subsequent effects on nitrogen cycling are likely to vary among ecosystems. Ecosystem inputs and losses of nitrogen, though not quantitatively significant in the short term, merit attention for their effects on nitrogen stocks in the long term. Over the timescale of CO₂ doubling, changes in nitrogen inputs and losses could affect carbon storage in the terrestrial biosphere. Again, however, while some experiments indicate that elevated CO₂ will decrease N losses (e.g., Hungate *et al.*, 1997c), others suggest that N losses will increase (e.g., Arnone and Bohlen, 1998). On the surface, qualitatively different results from different studies suggest that soil responses to elevated CO₂ are largely idiosyncratic, overriding the utility of any general patterns of response across ecosystems, if indeed any general patterns exist. However, some of the observed variation may be predictable (according to differences in plant species and in soil nutrient status, for example), and some is likely due to differences in techniques for measuring nitrogen cycling and in the timescale of the various experiments. In the future, researchers in this area should consider greater coordination, using the same techniques across many experiments. By doing so, we will be able to assess whether changes in soil nitrogen cycling in response to elevated CO₂ are general across many different systems, or whether they are idiosyncratic.

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