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Rhizosphere feedbacks in elevated CO_2

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Summary Understanding rhizosphere processes in relation to increasing atmospheric CO_2 concentrations is important for predicting the response of forest ecosystems to environmental changes, because rhizosphere processes are intimately linked with nutrient cycling and soil organic matter decomposition, both of which feedback to tree growth and soil carbon storage. Plants grown in elevated CO_2 substantially increase C input to the rhizosphere. Although it is known that elevated CO_2 enhances rhizosphere respiration more than it enhances root biomass, the fate and function of this extra carbon input to the rhizosphere in response to elevated CO_2 are not clear. Depending on specific plant and soil conditions, the increased carbon input to the rhizosphere can result in an increase, a decrease, or no effect on soil organic matter decomposition and nutrient mineralization. Three mechanisms may account for these inconsistent results: (1) the "preferential substrate utilization" hypothesis; (2) the "priming effect" hypothesis; and (3) the "competition" hypothesis, i.e., competition for mineral nutrients between plants and soil microorganisms. A microbial growth model is developed that quantitatively links the increased rhizosphere input in response to elevated CO_2 with soil organic matter decomposition. The model incorporates the three proposed mechanisms, and simulates the complexity of the rhizosphere processes. The model also illustrates mechanistically the interactions among nitrogen availability, substrate quality, and microbial dynamics when the system is exposed to elevated CO_2.

Keywords: competition hypothesis, forest ecosystem, nitrogen, preferential substrate utilization hypothesis, priming effect hypothesis.

Introduction

A continuous increase in atmospheric CO_2 concentration is one of the well-documented phenomena of global-scale environmental change (Keeling et al. 1989). The responses of ecosystems to elevated atmospheric CO_2 constitute critical feedback to the global carbon cycle. Many studies have shown that an increase in atmospheric CO_2 concentration results in increased primary productivity as measured by leaf-level or canopy-level gas exchange (Curtis 1996). The subsequent allocation and ultimate fate of this increased photosynthetically fixed carbon are important determinants of global carbon dynamics (Canadell et al. 1996). The partitioning of this extra carbon among pools with different turnover rates is a critical controlling step in carbon cycling and sequestration in terrestrial ecosystems.

Rhizosphere processes play an important role in carbon sequestration and nutrient cycling in terrestrial ecosystems (Helal and Sauerbeck 1989, Van Veen et al. 1991) and the rhizosphere has been identified as one of the key fine-scale components of the global carbon cycle (Coleman et al. 1992). Many important aspects of plant–soil interactions are mediated by rhizosphere processes, including plant nutrient acquisition (Uren and Reisennauer 1988), root colonization by rhizosphere microorganisms (Miller 1990, Baker 1991), and soil organic matter decomposition (Sallih and Bottner 1988, Cheng and Coleman 1990). Understanding rhizosphere processes in relation to the effects of increased CO_2 concentration is important for predicting the response of soil nutrients and organic matter to global environmental change.

Among many potential complex effects of elevated CO_2 on terrestrial ecosystems, three critical feedback loops involving rhizosphere processes can be identified (Figure 1). Increasing atmospheric CO_2 concentration is the initial driving factor, and primarily affects processes at the leaf or canopy level. The first feedback loop consists of four steps: (1) an increase in atmospheric CO_2 concentration causes an increase in plant primary production, a decrease in water use, and altered carbon allocation and other processes at the vegetation level; (2) these elevated-CO_2-induced changes at the vegetation level modify processes in the rhizosphere including root growth, root turnover, substrate input (or rhizodeposition), nutrient and water uptake, and microbial activities and associations; (3) altered rhizosphere processes lead directly to changes in soil nutrient availability; and (4) the changes in soil nutrient availability affect tree growth.

The second feedback loop also consists of four steps: (1) an increase in atmospheric CO_2 concentration causes changes at the vegetation level; (2) changes at the vegetation level result in alterations to processes in the rhizosphere; (3) altered rhizosphere processes either increase or decrease soil organic matter (SOM) decomposition; and (4) changes in SOM decomposition cause changes in soil carbon storage or loss to the atmosphere.

The third feedback loop consists of five steps: (1) an increase in atmospheric CO_2 concentration causes changes at the vege-

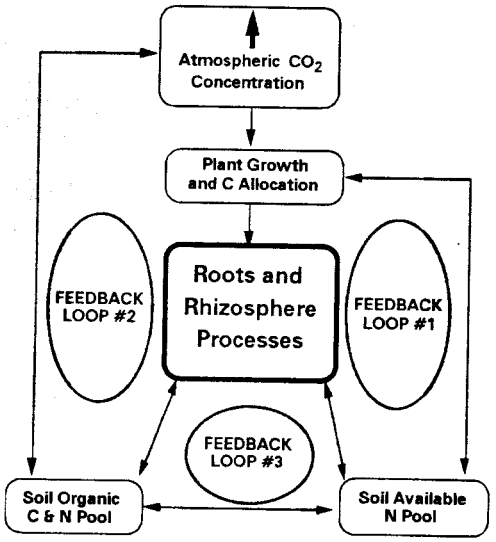

Figure 1. Relationship between the concentration of atmospheric CO_2 and rhizosphere processes, and the important role of rhizosphere processes in terrestrial carbon and nitrogen cycling.

tation level; (2) changes at the vegetation level result in alterations to processes in the rhizosphere; (3) altered rhizosphere processes may either increase or decrease SOM decomposition; (4) changes in SOM decomposition cause changes in soil nutrient mineralization/immobilization; and (5) soil nutrient dynamics affect tree growth.

This paper reviews published data on C input to the rhizosphere in response to elevated CO_2. A simple model simulating microbial growth and its effect on nitrogen availability to tree growth is used to analyze how this altered C input to the rhizosphere affects SOM decomposition and nutrient availability.

Carbon input to the rhizosphere in elevated CO_2

Root-derived carbon (i.e., rhizodeposition) is considered to be the driving force for most rhizosphere activities. Plants grown in elevated CO_2 often exhibit increased growth and disproportional increases in C allocation to roots (Norby et al. 1986, Curtis et al. 1990, Rogers et al. 1992, 1994, Pregitzer et al. 1995), total rhizosphere respiration and rhizodeposition (Whipps 1985, Kuikman et al. 1990, Billes et al. 1993). By using carbon isotope tracers in CO_2 enrichment experiments at the small-pot scale, it has been demonstrated that, compared to ambient CO_2 concentrations, elevated CO_2 increases the amount of carbon allocated to the rhizosphere by enhancing root deposition (Ineson et al. 1996, Hungate et al. 1997), or total rhizosphere respiration (Gorissen 1996, Hungate et al. 1997, Cheng and Johnson 1998). In general, total carbon input to the rhizosphere is significantly increased when plants are grown in elevated CO_2 (Table 1).

Several studies suggest that more carbon is fixed as a result of a large increase of leaf-level or canopy-level photosynthesis in systems exposed to elevated CO_2 than can subsequently be accounted for in plant biomass or soils. The carbon unaccounted for is often called "the locally missing carbon" to distinguish it from the missing carbon at the global scale. In an alpine grassland subjected to three years of CO_2 enrichment, there was a 41% increase in CO_2 uptake, but no aboveground biomass increase was observed and only a slight increase in belowground biomass was detected (Körner et al. 1996). In a study of yellow poplar (*Liriodendron tulipifera* L.) subjected to continuous exposure to ambient or elevated concentrations of atmospheric CO_2 for three growing seasons, Norby et al. (1992) reported that there was no significant effect of CO_2 concentration on dry mass production, despite a sustained increase in photosynthesis and reduced foliar respiration. It has been hypothesized that the so-called "locally missing carbon" is partly due to increases in carbon allocation to some unmeasured belowground components such as root turnover, root respiration, and root exudation. This hypothesis is supported by results of several recent studies with herbaceous plants. For example, Cheng and Johnson (1998) have shown that elevated CO_2 substantially increases C input to the rhizosphere as a result of enhanced root exudation and rhizosphere respiration. In a continuous ^{14}C-labeling study with wheat, Lekkerkerk et al. (1990) reported that rhizosphere respired C from wheat plants grown in elevated CO_2 significantly increased and accounted for a substantial portion of the whole C economy. Hungate et al. (1997) reported that, in a microcosm experiment with mixed grasses, elevated CO_2 significantly enhanced total rhizosphere deposition. However, all the evidence supporting this hypothesis is from studies with herbaceous plants. Whether this hypothesis holds for trees remains to be tested.

Recent results suggest that the degree of CO_2 enhancement of rhizosphere respiration is much higher than the enhancement of root biomass. Cheng and Johnson (1998) reported that, compared with the ambient CO_2 treatment, wheat rhizosphere respiration rate increased 60% and root biomass only increased 26% in response to elevated CO_2. In a continuous ^{14}C-labeling study with wheat, Lekkerkerk et al. (1990) reported that plants grown in elevated CO_2 produced 74% more rhizosphere-respired C and only 17% more root biomass than plants grown in ambient CO_2. Data obtained from a microcosm experiment with mixed grasses indicated that elevated CO_2 enhanced total rhizosphere deposition by 56% and root biomass by less than 15% (Hungate et al. 1997). Two mechanisms could explain these results. First, roots from plants grown in elevated CO_2 exuded more C and had higher turnover rates than roots grown in ambient CO_2, resulting in a more than proportional increase in total rhizosphere respiration in elevated CO_2. Second, elevated CO_2 enhanced rhizosphere microbial associations, resulting in higher rhizosphere microbial activities per unit of root growth in elevated CO_2 than in ambient CO_2.

Several lines of evidence support the first mechanism. Using the isotopic trapping method, Cheng et al. (1993, 1994) found an approximately 60% increase in soluble C concentration in the rhizosphere when wheat plants were grown in elevated CO_2 compared to ambient CO_2, indicating that roots from plants grown in elevated CO_2 exuded more soluble C (Cheng and Johnson 1998). Pregitzer et al. (1995) found that root turnover rates were higher for plants grown in elevated CO_2 than for plants grown in ambient CO_2. However, the amount of extra C

Table 1. Effect of elevated CO_2 on rhizodeposition. Abbreviations: SRD = specific rhizodeposition, or total deposition per gram of roots; Rhizo CO_2 = rhizosphere respiration; NE = no significant effect; ND = not determined; and a = increased.

Plant sp.	Conditions	Rhizodeposition	Rhizo CO_2	Soil residue	SRD	Reference
Wheat	Micro-^{14}C	a	a	a	a	Kuikman et al. 1990
Wheat	Micro-^{14}C	a	a	a	NE	Billes et al. 1993
Sweet chestnut	Micro-^{14}C-PL	a	a	ND	ND	Rouhier et al. 1996
Wheat	Micro-^{14}C-PL	a	a	a	ND	Paterson et al. 1996
Rye grass	Micro-^{14}C-PL	NE	NE	ND	ND	Paterson et al. 1996
Wheat	Micro-^{13}C	a	a	a	a	Cheng and Johnson 1998
Yellow birch	Micro-^{13}C	a	ND	a	ND	Ineson et al. 1996
Grasses	Micro-^{13}C/OTP-^{13}C	a	a	a	ND	Hungate et al. 1997

input to the rhizosphere resulting from the enhanced root turnover in elevated CO_2 is predicted to be low in most short-term tracer studies (e.g., Lekkerkerk et al. 1990, Hungate et al. 1997, Cheng and Johnson 1998) because the life span of the roots is probably longer than the duration of the experiment (Eissenstat and Yanai 1997). Therefore, enhanced root exudation was probably the major component of this extra C input to the rhizosphere in these short-term experiments. However, enhanced root turnover in response to CO_2 in forest ecosystems might be important because root turnover is one of the principal processes responsible for C input in some forests (Hendrick and Pregitzer 1992). The second mechanism is widely supported by indirect evidence. Elevated CO_2 increases both percent infection of vesicular-arbuscular mycorrhizae (Monz et al. 1994) and percent infection of ectomycorrhizae (Norby et al. 1987, O'Neill et al. 1987, O'Neill 1994, Ineichen et al. 1995, DeLucia et al. 1997, Rygiewicz et al. 1997). Elevated CO_2 also increases symbiotic N_2-fixation across several types of associations (Phillips et al. 1976, Masterson and Sherwood 1978, Norby 1987, Arnone and Gordan 1990, Thomas et al. 1991, Hibbs et al. 1995, Tissue et al. 1997). However, direct evidence of higher rhizosphere symbiotic activities per unit of root growth in elevated CO_2 is lacking.

Rhizosphere effects on decomposition and nutrient availability

The fate and function of the extra carbon input to the rhizosphere in elevated CO_2 are not clear. There are two processes whereby increased rhizosphere C could have important impacts on carbon cycling (Canadell et al. 1996). First, the additional C is utilized by microorganisms and partially converted into SOM, thereby increasing soil C storage. Second, the extra C alters soil microbial processes by providing needed substrates, thereby either stimulating SOM decomposition as a result of the so-called "priming effect" (stimulation of SOM decomposition caused by the addition of labile substrates, Dalenberg and Jager 1989) (Billes et al. 1993, Zak et al. 1993) or suppressing SOM decomposition resulting from microbial immobilization (Diaz et al. 1993).

The effects of elevated CO_2 on soil N availability have important effects on ecosystem C accumulation because: (1) N is the most frequently limiting nutrient in the northern hemisphere, and (2) soil N pools are large relative to vegetation N requirements, with only a small fraction (typically 1% or less) being available for uptake at any given time. There is some evidence that elevated CO_2 can affect soil carbon and nitrogen mineralization through rhizosphere effects. Körner and Arnone (1992) found a reduction in soil C and increases in soil respiration and nitrate leaching in an artificial tropical ecosystem subjected to elevated CO_2. They attributed these results to an increased rate of soil organic matter decomposition in the rhizosphere. Similarly, Zak et al. (1993) found increased microbial biomass C and N mineralization in the rhizosphere soils of *Populus grandidentata* Michx. seedlings subjected to elevated CO_2. These findings have implications for the ability of rapidly growing forests to acquire more N from the soil in times of high N demand. On the other hand, if elevated CO_2 causes rhizodeposition of labile C with a high C/N ratio, it may increase microbial N demand and the immobilization rather than the mineralization of available N (Diaz et al. 1993), potentially causing a nutrient feedback in the opposite direction of that posed by Zak et al. (1993).

By carrying out microcosm experiments of grassland assemblages at ambient and elevated CO_2 for approximately a year, Diaz et al. (1993) found that assemblages grown in elevated CO_2 exhibited significant increases in soil microbial biomass carbon and nitrogen, whereas no increase in aboveground plant biomass was found. Based on these results, Diaz et al. (1993) postulated that (1) elevated CO_2 increased carbon input to the rhizosphere, (2) this increased carbon input stimulated the growth of rhizosphere microorganisms, and (3) this increased microbial growth immobilized available nutrients in the soil, thereby resulting in a reduction in the amount of nutrient available (i.e., nitrogen) to plant growth, and (4) this reduced nutrient availability led to a reduction in plant growth response to elevated CO_2. Therefore, a negative feedback mechanism was proposed between plant growth and the increased carbon input to the rhizosphere in elevated CO_2.

In a study of *Populus grandidentata* growing in open-top chambers in the presence of ambient or elevated CO_2 for approximately two years, Zak et al. (1993) found that plant growth, microbial biomass in the rhizosphere, and nitrogen mineralization rate in the rhizosphere soil were significantly increased by elevated CO_2. They postulated that (1) elevated CO_2 increased carbon input to the rhizosphere, (2) this in-

creased carbon input stimulated the growth of rhizosphere microorganisms, and (3) this increased microbial growth stimulated nutrient mineralization in the soil, thereby increasing the amount of available nutrient to plant growth, and (4) this increased nutrient availability led to a further enhancement in plant growth response to elevated CO_2. Therefore, a positive feedback mechanism was proposed between plant growth and the increased carbon input to the rhizosphere in elevated CO_2.

Increasing atmospheric CO_2 changes the effect of rhizosphere processes on SOM decomposition in several possible directions. Although an increased rate of SOM decomposition in elevated CO_2 has been assumed to be more likely (Luxmoore 1981, Körner and Arnone 1992, Billes et al. 1993, Zak et al. 1993), stimulatory (Billes et al. 1993, Zak et al. 1993), suppressive (Kuikman et al. 1990, Rouhier et al. 1994), and neutral (Liljeroth et al. 1990, Lin et al. 1998) results have all been reported (Table 2). Cheng and Johnson (1998) reported that the status of soil nitrogen (with or without N fertilization) was an important modifier that switched the direction of the elevated CO_2 effect on SOM decomposition. Elevated CO_2 increased SOM decomposition in the nitrogen-addition treatment but decreased SOM decomposition in the treatment lacking nitrogen. In a microcosm study with mixed grasses using ^{13}C pulse labeling method, Hungate et al. (1997) reported that elevated CO_2 increased SOM decomposition only in the nitrogen-addition treatment, and elevated CO_2 did not significantly affect SOM decomposition in the treatment without nitrogen fertilization. On the other hand, in a microcosm study with similar grass species using a natural ^{13}C tracer technique, Cardon (1996) reported that elevated CO_2 decreased SOM decomposition in the nitrogen-fertilized treatment, but did not significantly affect SOM decomposition in the treatment without nitrogen fertilization. In a growth chamber study with spring wheat grown in well-fertilized soils using a continuous ^{14}C-labeling technique, Kuikman et al. (1990) reported that elevated CO_2 decreased SOM decomposition at the last sampling (49 days) but not at the first sampling (22 days). In a microcosm study using yellow birch (*Betula alleghaniensis* Britt.), Berntson and Bazzaz (1997) found that elevated CO_2 increased SOM decomposition (as indirectly indicated by nitrogen mineralization) during the initial period, but decreased SOM decomposition during the later period, suggesting that temporal variation changed the direction of the process. Although it is probably not meaningful to generalize from these data, which were obtained under diverse experimental conditions, these various results indicate that the effect of elevated atmospheric CO_2 on SOM decomposition is dependent on the plant–soil system and is not unidirectional. Among many potentially relevant factors, soil mineral nutrition (Cardon 1996, Hungate et al. 1997, Cheng and Johnson 1998), plant species (Hungate et al. 1996, Paterson et al. 1996), and temporal variation (Kuikman et al. 1990, Berntson and Bazzaz 1997), were the important determinants of the direction and possibly the magnitude of the effect of elevated atmospheric CO_2 on SOM decomposition.

Three mechanistic hypotheses are considered to explain these results: (1) the "preferential substrate utilization" hypothesis (Merckx et al. 1987, Lekkerkerk et al. 1990, Liljeroth et al. 1990); (2) the "priming effect" hypothesis (Dalenberg and Jager 1989, Nicolardot et al. 1994); and (3) the "competition" hypothesis—competition for mineral nutrients between plants and soil microorganisms (Schimel et al. 1989, Ehrenfeld et al. 1997).

The "preferential substrate utilization" hypothesis states that, given abundant mineral nutrient supply, soil microorganisms prefer labile root-derived C to soil-derived carbon. As a result, there is decreased SOM decomposition when more root-derived C is produced in elevated CO_2. However, if mineral nutrients are in short supply, soil microorganisms prefer nutrient-rich SOM to root-derived C, resulting in increased SOM decomposition when more root-derived C is produced in elevated CO_2. This hypothesis emphasizes the role of soil mineral nutrition, and assumes that all root-derived materials have a much higher C/N ratio than the SOM. The results of Cardon (1996) and Kuikman et al. (1990) showing that elevated CO_2 in the fertilized treatment reduced SOM decomposition seem to support this hypothesis. However, the hypothesis is in conflict with the results of Hungate et al.

Table 2. Effect of elevated CO_2 on nitrogen availability, soil microbial biomass, and soil organic matter (SOM) decomposition. (OTC = open-top chamber; Rhizo = rhizosphere soil; GH = green house; d = day; m = month; y = year; NE = no significant effect; ND = not determined; a = increased; and b = decreased).

Plant species	Conditions	Duration	Microbial biomass	N availability	SOM decomposition	Reference
Grasses	OTC	5 m	ND	ND	b	Cardon 1996
Grasses	Microcosm	84–112 d	a	b	ND	Díaz et al. 1993
Populus	OTC/Rhizo	152 d	a	a	a	Zak et al. 1993
Grasses, CA	OTC	5 m	a	a	ND	Hungate et al. 1996
Cynodon dactylon (L.) Pers.	Microc/Rhizo	21 d	NE	ND	ND	Paterson et al. 1996
Pinus ponderosa Dougl. *ex* Laws.	OTC	5 y	a	ab	ND	Cheng et al. unpublished data
Tropical spp.	GH	1 y	ND	a	a	Körner and Arnone 1992
Triticum aestivum L.	Microcosm	28 d	ND	a	a	Billés et al. 1993
T. aestivum	Microcosm	22–49 d	ND	b	b	Kuikman et al. 1990
Castanea	Microcosm	14 d	ND	b	b	Rouhier et al. 1994
T. aestivum	Microcosm	42 d	ND	ND	ab	Cheng and Johnson 1998

(1997) and Cheng and Johnson (1998) who found that elevated CO_2 in the fertilized treatment stimulated SOM decomposition.

The "priming effect" hypothesis states that the extra input of labile root-derived C in elevated CO_2 initially decreases SOM decomposition as a result of the increase in microbial growth and immobilization of mineral nutrients, but that it stimulates SOM decomposition and nutrient release later because of the turnover of this newly grown microbial biomass. Further, it states that the quality of the root-derived substrates is an important determinant of the timing and the magnitude of this "priming effect." This hypothesis emphasizes the temporal microbial dynamics and the quality of the root-derived substrates. Potentially, this hypothesis could explain all of the results mentioned above. Unfortunately, information on microbial dynamics and root exudate quality is difficult to obtain and rarely available.

The "competition" hypothesis states that the extra root-derived C input as a result of increased root growth or activities in elevated CO_2 decreases SOM decomposition under mineral nutrient-limited conditions, and increases SOM decomposition under conditions of adequate mineral nutrient supply. Both soil nutrition and the competition for mineral nutrients between roots and soil microorganisms are important in the "competition" hypothesis. The results of Hungate et al. (1997) and Cheng and Johnson (1998) showing that elevated CO_2 in the fertilized treatment stimulated SOM decomposition seem to support this hypothesis. However, the hypothesis is in conflict with the results of Cardon (1996) and Kuikman et al. (1990) showing that elevated CO_2 in the fertilized treatment reduced SOM decomposition. The prediction of the "competition" hypothesis is opposite to that of the "preferential substrate utilization" hypothesis.

Probably, none of the three hypotheses, alone, explains all the experimental results. However, all three postulated mechanisms may operate simultaneously, resulting in an array of outcomes. A computer model quantitatively incorporating all three mechanisms would improve understanding of this issue.

A model of soil microbial growth in elevated CO_2

In this section, I describe a simple model developed to simulate the effects of elevated CO_2 on soil microbial biomass and N dynamics, and the linkage between the increase in CO_2 concentration and soil organic matter decomposition. Soil microbial biomass has been used as a sensitive indicator of system changes induced by perturbations such as elevated atmospheric CO_2 (Zak et al. 1993), tillage practices (Carter 1986, Doran 1987), soil organic matter decomposition (Ladd et al. 1981, Follett and Schimel 1989, Van Veen et al. 1989), and climatic regimes (Insam et al. 1989, Insam 1990). The rapid response of microbial biomass to differences in detritus input suggests that this fraction can be used to indicate long-term trends in total soil C concentrations. Many existing models consist of multiple compartments (e.g., Jenkinson and Rayner 1977, Paustian et al. 1992, Post et al. 1992, Parton et al. 1995), and accurate parameterization of these models is often difficult. The approach adopted here uses a simplified version of the microbial biomass model developed by Hyvönen et al. (1996).

Because soil microbial growth is mainly limited by the amount of available substrate (Anderson and Domsch 1978), the increase of soil microbial biomass in elevated CO_2 is mainly controlled by the amount of extra substrate input. Thus, the net effect of elevated atmospheric CO_2 on soil microbial biomass C and N can be expressed as:

$$dM_c/dt = Sa - M_c b, \quad (1)$$

$$dM_n/dt = M_c/R_m, \quad (2)$$

where M_c is the net change of microbial biomass in response to elevated CO_2; S is the net change of substrate input into the soil in response to elevated CO_2; parameter a is the assimilation efficiency of microbial growth with S as the substrate; parameter b is the net microbial biomass turnover rate; M_n is the net change in microbial biomass N; and parameter R_m is the C/N ratio of the microbial biomass.

The value of a has been shown by Ågren and Bosatta (1996) to be a constant for a range of substrate types and physical conditions. I therefore use their value of $a = 0.25$. The value of b is reported to be in the range of 0.15 to 4 per year depending on environmental conditions (Jenkinson and Rayner 1977, Voroney and Paul 1984, Jenkinson et al. 1992, Goyal et al. 1993). Published values of R_m are mostly in the range of 6 to 15 (Cheng and Virginia 1993), depending on the composition of the microbial community.

A similar model can be applied to simulate microbial growth utilizing original soil organic matter as substrates. Linking the two sister models, the mechanisms controlling the interactions between elevated CO_2 and soil organic matter decomposition can be further analyzed. If the increased rhizosphere substrate input in response to elevated CO_2 reduces microbial utilization of original soil organic matter (the variable S in the original organic matter model), a negative feedback exists as the "substrate preference" hypothesis states, so that soil organic matter decomposition decreases. If the increased rhizosphere input in response to elevated CO_2 results in an increase in overall microbial biomass turnover rate, or a higher parameter b, a positive feedback exists as the "priming" hypothesis states, so that soil organic matter decomposition increases. Under highly mineral nutrient-limited conditions, the increased rhizosphere input in response to elevated CO_2 may intensify the competition for mineral nutrients between roots and microorganisms, and result in a decrease in C substrate usage (S), a reduced substrate utilization efficiency (parameter a), and a lower amount of microbial biomass. This pattern fits the "competition" hypothesis well. Although this is a highly simplified model, it serves to illustrate some of the important mechanisms governing the complex interactions between elevated CO_2 and soil organic matter decomposition. The overall outcome of decomposition depends on the balance among the three kinds of controls.

The model can be used to link the net change of available N and substrate quality when trees are grown in elevated CO_2.

The net change of mineral N can be expressed as:

$$dN/dt = M_n b + SR_s - Sa/R_m, \quad (3)$$

where N is the amount of mineral N, R_s is the C/N ratio of the extra substrate input, $M_n b$ is N mineralized as a result of microbial biomass turnover, SR_s is N mineralized as a result of microbial utilization of the extra input, and Sa/R_m is N immobilized as a result of microbial growth.

The model is based on the following assumptions: (1) the extra substrate input to the soil in response to elevated CO_2 is linearly proportional to the rate of primary production (This is based on the concept of a constant CO_2 fertilization factor, see Norby et al. 1995, 1996, Luo et al. 1996.); (2) the primary production of the trees follows an exponential pattern through time; (3) the value of microbial assimilation efficiency, a, is 0.25; and (4) the value of microbial biomass turnover rate, b, is 0.5 per year, which is higher than the value of 0.41 at Rothamsted and much lower than the value of 4 for a tropical region in Brazil.

In this simple model, two parameters, the C/N ratio of the extra input caused by increasing CO_2 concentrations and the C/N ratio of the extra soil microbial biomass, significantly influence N mineralization and immobilization dynamics. The higher C/N ratio of the extra input favors N immobilization initially, whereas the higher C/N ratio of the extra soil microbial biomass favors N mineralization (Figures 2 and 3). If elevated CO_2 alters either the C/N ratio of the extra input or the C/N ratio of microbial biomass, soil N mineralization and immobilization dynamics will be affected too. This also helps explain why nitrogen fertilization affects the interaction between elevated CO_2 and soil organic matter decomposition (Cardon 1996, Hungate et al. 1997, Cheng and Johnson 1998).

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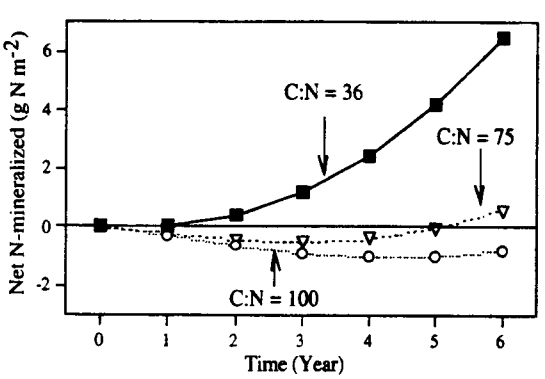

Figure 2. The effect of the C/N ratio of the extra rhizosphere input in response to elevated CO_2 on mineral N dynamics. The C/N ratio of the extra soil microbial biomass is set at 10 for all simulations.

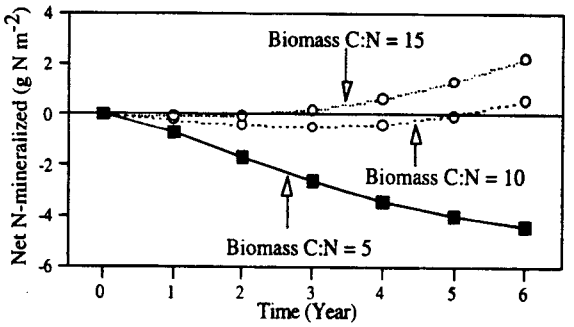

Figure 3. The effect of the C/N ratio of the extra soil microbial biomass on N dynamics. The C/N ratio of the extra input is set at 75 for all simulations.

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