THE IMPACT OF ATMOSPHERIC CO_2 ENRICHMENT ON THE BIOGEOCHEMISTRY OF C AND N IN A MEDITERRANEAN FOREST ECOSYSTEM

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ABSTRACT - Elevated atmospheric CO_2 can affect the dynamics of soil organic matter (SOM), and consequently C and N cycling in terrestrial ecosystems. This study evaluates the effect of enhanced CO_2 on substrate quality and subsequent rates of its decomposition, and on soil organic matter by using a plant litter-SOM continuum around a mineral CO_2 spring in Central Italy. Elevated CO_2 did not change leaf litter quality or decomposition; neither did it affect chemical composition of SOM and C decomposition in the soil. Yet, total C and N pool sizes in the forest floor were doubled at elevated CO_2, probably as a result of increased plant production. This suggests that elevated CO_2 increases the soil-sink of atmospheric CO_2. Nitrogen immobilization in the forest floor was lower under elevated than ambient CO_2, whereas N mineralization in the A horizon remained unaffected.

This study casts doubt on the common idea that elevated CO_2 changes litter quality, and thereby slows down decomposability of litter and N release, but strongly suggests that elevated CO_2 increases SOM pools via higher litter quantity through increased net primary production.

Keywords: Climate Change, litter quality and decomposition, Mediterranean ecosystems, mineral CO_2 springs, soil organic matter

INTRODUCTION

Carbon dioxide is an essential substrate for living plants, which link two main C reservoirs: atmospheric C with soil C. It is also an important greenhouse gas, which contributes to global warming. Human consumption of fossil fuels and forest clear-cutting in the tropics has caused approximately a 28 % increase in the atmospheric CO_2 concentration since the beginning of the Industrialization Revolution in 1700. Increasing rates of consumption of fossil fuels and deforestation will result in a continuing rise in CO_2 concentrations in the coming decades (IPCC 1995; Schimel 1995). Burning of fossil fuel and deforestation has disturbed the global C cycle so that the imbalance between global C sources and known sinks implies the presence of an unknown C sink (the so-called "missing CO_2"). The missing CO_2 may be trapped in soils and vegetation via CO_2 fertilization, forest regrowth in the northern hemisphere and atmospheric N deposition (Gifford 1994; Schimel 1995).

The rise in CO_2 concentration, and related greenhouse effect, is expected to lead to an increase in global temperature of 1-3.5 °C by the end of the next century (IPCC 1995). Elevated atmospheric CO_2 concentrations and global temperature may result in an array of

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changes in terrestrial ecosystems, varying from short-term physiological changes (Eamus and Jarvis 1989; Poorter 1993; Luxmoore *et al.* 1993) to long-term modification in pools of soil organic matter (SOM) and nutrients (O'Neill and Norby 1996; Hungate *et al.* 1997). Global climate change may also have some direct or indirect consequences for the pedosphere. While global warming may accelerate soil carbon decomposition, elevated CO_2 may change the composition and dynamics of soil organic matter (SOM) via (1) increased rates of addition of plant litter to the soil (2) alterations in litter quality and (3) enhanced rhizodeposition through the allocation of more C to root systems. O'Neil and Norby (1996), McGuire *et al.* (1995), Ball (1997) and Cotrufo *et al.* (1998) have reviewed a great deal of the literature on possible changes in litter quality due to a doubling in the atmospheric CO_2. On the other hand, enhanced CO_2 may decrease stomatal conductance (Eamus and Jarvis 1989; Bettarini *et al.* 1998), and hence reduce transpiration while increasing water use efficiency (WUE). Reduced transpiration may increase soil water availability, which stimulates decomposition and mineralization in surface soils, in particular in water-limited ecosystems such as arid and semi-arid zones.

Because soil plays a central role in plant growth and in global C and N cycles, it is essential to advance our knowledge and understanding of the effect of elevated CO_2 on SOM. To investigate these effects, long-term experiments are necessary. Natural CO_2 springs provide a convenient and useful environment to carry out such long-term studies on ecosystem functioning, especially with respect to effects on soil C.

The aim of this chapter is to discuss the long-term impacts of elevated CO_2 on the dynamics of soil organic matter in a Mediterranean ecosystem which has been exposed to elevated CO_2 for an extended period. In this chapter, we present results from natural CO_2 springs where the effects of elevated CO_2 on plant litter (quality and decomposability) and soil organic matter (pools and decay) continuum were studied. The important feedbacks that SOM may impose on plant growth and atmospheric CO_2 are speculated upon. By obtaining soil data around CO_2 springs, we also attempt to answer several fundamental questions, such as "*Will elevated CO_2 affect quality and decomposability of litter of mature plants growing in N-limited ecosystems exposed to long-term elevated CO_2 for?*" and "*Are such CO_2 effects on litter quality reflected in soil C dynamics?*"

MATERIALS AND METHODS

Research site

The studied location is a Mediterranean forest ecosystem. These ecosystems are the subject of concern in IGBP-GCTE (the International Geosphere-Biosphere Programme - Global Change and Terrestrial Ecosystems) because of their vulnerability to global climate change (IGBP 1994). The study site is located near the village of Laiatico, approximately 35 km south-east of Pisa, Italy (43° 26'N, 10° 42'E, at 190-240 m above sea level, with annual rainfall of 830 mm; average yearly temperature of 15 °C). The area (ca. 0.9 ha) is a sloping forested region with an irregular and rough surface. Soils in the area are calcareous, developed from Tertiary marl. The soil pH(H_2O) is 6.9 in the topsoil and above 7.3 in the subsoil. The soil texture is silty clay loam in the topsoil and silty clay in the subsoil. The soil is covered by a litter layer (F+HA) of varying thickness. The study area is

a typical, semi-natural coppiced Mediterranean woodland which was last cut about 25 years ago. The vegetation comprises *Quercus ilex* L., *Quercus cerris* L., *Fraxinus ornus* L., *Quercus pubescens* Willd., with shrubs such as *Erica arborea* L. and *Arbutus unedo* L.. The understory is dominated by the vine *Smilax aspera* L.
The CO_2 spring, consisting of one major vent and a number of smaller ones within a circle of 5 meters, is situated at the bottom of a gully. This results is a CO_2 gradient from ambient (350 ppm) to about 600 ppm at the vent (Raiesi, 1998). Because factors other than atmospheric CO_2 concentration contribute to spatial differences in soil properties including SOM within the valley, a comparable transect (ambient CO_2, similar parent material, slope-soil hydrological conditions, and vegetation) was selected for control area.

Litter sampling and analysis
Senescent leaf litter from oak (namely *Quercus cerris*, *Quercus pubescens* and *Quercus ilex*), ash (*Fraxinus ornus*) and one understory species(*Smilax aspera*), which contribute significantly to litter input to the soil, were collected from an area enriched long-term to CO_2 concentrations of c.550 ppm, and from a control area with 360 ppm CO_2. Litter samples were taken manually from both trees and soil surface. The samples were air-dried, mixed and ground to pass through a 1-mm sieve for quality analysis. Litter quality parameters such as N (all plant species), lignin and cellulose (only *Q. cerris* and *Q. pubescens*) and polyphenolic compounds (only *Q. cerris*, *Q. pubescens* and *S. aspera*) were determined in ground material (Anderson and Ingram 1993; Rowland and Roberts 1994; van Lagen 1996). The decomposition rate of litter was studied using a litter bag experiment (12 months) and laboratory incubations (3 months). In laboratory incubations, N mineralization in litter samples was measured (125 days). For *S. aspera*, incubation experiments lasted 48 (C incubation) and 60 days (N incubation).

Soil sampling and analysis
Soil samples were collected along a CO_2 gradient of decreasing atmospheric CO_2 levels from the source to ambient (360 ppm) between 50 to 100 m from the vent (for a map of CO_2 concentrations and sample locations, see Raiesi et al., 1997; Raiesi, 1998). Topographically similar transects were selected and sampled at the control area. Undisturbed soil cores of 26 profiles (17 in the vet area, 9 in the control area) were sampled with a teethed auger (20 cm high and 8 cm ϕ). The cores were sectioned vertically to obtain separate samples from the F and HA horizons in the forest floor and from 0-10 and 10-20 cm depths in the mineral soil. Contents of C and N were determined to calculate the pools of C and N on the basis of measured soil bulk density. Additionally, the thickness of the forest floor (F and HA layers) as a function of atmospheric CO_2 concentration was measured. C and N decay rates were studied by tracking CO_2 evolution from, and by extracting N mineralized in, samples incubated at 20°C in the laboratory for 15 (C mineralization) or 30 (N mineralization) days.

Table 1. Leaf litter quality parameters of Mediterranean species growing under elevated and ambient CO_2 levels at the Laiatico mineral CO_2 spring. (from Raiesi *et al.* 1997a,b; Raiesi, 1998, 1999).

	Concentration (%)				Ratios (-)			
	N	Lignin	Cellulose	Polyph.[†]	C/N	Lignin/N	Cellulose/N	Polyph.[†]/N
***Quercus cerris** (n=2)*								
Elevated CO_2 area	0.72	27.2	19.7	19.3	77.7	38.0	27.4	27.0
Ambient CO_2 area	0.76	26.8	20.6	20.5	73.6	35.0	26.9	26.6
***Q. pubescens** (n=2)*								
Elevated CO_2 area	0.81	19.3	22.8	21.1	65.2	23.9	28.3	26.1
Ambient CO_2 area	0.84	18.5	21.4	19.7	63.2	22.9	25.8	24.0
***Smilax aspera** (n=3)*								
Elevated CO_2 area	1.07	n.d.	n.d.	0.86	52.6	n.d.	n.d.	0.81
Ambient CO_2 area	1.01	n.d.	n.d.	0.82	56.1	n.d.	n.d.	0.81
***Q. ilex** (n=3)*								
Elevated CO_2 area	0.75	n.d.	n.d.	n.d.	72.8	n.d.	n.d.	n.d.
Ambient CO_2 area	0.75	n.d.	n.d.	n.d.	72.2	n.d.	n.d.	n.d.
***Fraxinus ornus** (n=3)*								
Elevated CO_2 area	0.75	n.d.	n.d.	n.d.	69.8	n.d.	n.d.	n.d.
Ambient CO_2 area	0.76	n.d.	n.d.	n.d.	69.2	n.d.	n.d.	n.d.

[†] Polyphenols; n.d., not determined.

RESULTS AND DISCUSSION

Elevated CO_2 effect on litter chemistry and turnover

We studied changes in litter chemistry of plants following exposure to long-term elevated CO_2 and subsequent effects on C and N mineralization. The chemical composition (e.g. N, lignin, cellulose and polyphenols) and compounds-to-N ratios of *Quercus cerris* and *Q. pubescens* and *Smilax aspera* litter from high-CO_2 were not significantly different from those from ambient CO_2 (Tab. 1). Similar results were obtained with *Quercus ilex* L. and *Fraxinus ornus* L. leaf litter.

Carbon and nitrogen concentrations, and C/N ratios of non-scenescent leaves of *S. aspera* were unaffected by CO_2 level (Tab. 2). Also the re-translocation of nitrogen during senescence (Table 2) appears unaffected by CO_2 level. This means that a decrease in effeciency of this translocation, as observed in other species (Arp and Berendse, 1993) is not found in *Smilax* exposed to long-term high CO_2 concentrations.

As expected from the litter quality data, rates of decomposition (measured with litter bags) in ambient and elevated CO_2 were similar in *Q. cerris* and *Q. pubescens*. Three months of incubation in the laboratory indicated that litter decomposition of neither species was affected by elevated CO_2 (Tab. 3). Similarly, decomposition under laboratory conditions in *S. aspera* litter was unaffected by the CO_2 level at which the plants were grown. N mineralization in leaf litter was monitored for 125 days (oaks) or 60 days (*S. aspera*). Although, the initial N mineralization in litter was higher at elevated CO_2 than that at ambient CO_2 (Fig. 1), it was not affected by CO_2 in the long term (Tab. 3), again in accordance with the absence of a CO_2 impact on litter chemistry.

Results from long-term experiments around CO_2 springs provided evidence that increases in the atmospheric CO_2 concentration do not influence substrate quality, and therefore it is unlikely that rising CO_2 levels will affect C and N turnover rates of litter in terrestrial ecosystems. The lack of a CO_2-effect on litter decomposition, found in this type of system, corresponds with recent field observations in boreal forests (Verburg 1998), lowland calcareous grasslands and lowland wet tropical forests (Hirschel *et al.* 1997), tall grass prairie (Kemp *et al.* 1994; Owensby *et al.* 1993, 1996), temperate deciduous forest (O'Neill and Norby 1996), and some agricultural crops (Henning *et al.* 1996; Taylor and Ball 1994).

Table 2. N content and C/N ratio of fresh green leaves, and N re-translocation before abscission in *Smilax aspera* growing at ambient and naturally enriched CO_2 concentrations around the Laiatico CO_2 spring.

CO_2 level (ppm)	N (%)	C/N (-)	N re-translocation (%)
543	1.37	36.8	21.8
373	1.32	38.9	21.0
363	1.31	39.3	21.9

The absence of any CO_2 effect on litter quality could be due to either increased nutrient uptake by roots (Day *et al.* 1996) or the down-regulation of photosynthesis (Ryle *et al.* 1992;

Grulke *et al.* 1993; El Kohen *et al.* 1993; Miglietta *et al.* 1995; Oechel and Vourlitis 1996; Hättenschwiler and Körner 1996) at elevated CO_2. In N-limited systems, plants may take up inorganic N directly through absorption of amino acids (Chapin *et al.* 1993; Keilland 1994) or use atmospheric N deposition more efficiently when grown at elevated CO_2. Decreased efficiency of N-withdrawal under CO_2-enrichment (Arp and Berendse 1993) may be another mechanism by which plants would counteract the N-dilution of increased C fixation rates under elevated CO_2, but it seems that this mechanism can not explain unchanged litter quality with CO_2 enrichment.

Our long-term CO_2 studies cast doubt on the general concept that elevated CO_2 changes the litter quality of plants, and thereby slows down decomposition of litter and N dynamics. Although a number of authors judge that the CO_2 effect on litter quality is still undecided, many field studies indicate that elevated CO_2 does not change litter quality, and that therefore rates of C decomposition are not expected to change (Norby *et al.* 1995; O'Neill and Norby 1996; Koch and Mooney 1996; Henning *et al.* 1996; Randlett *et al.* 1996; Hirschel *et al.* 1997; Verburg 1998; Mooney *et al.* 1998). The results of our study contribute to recent findings that there is no convincing evidence that leaf litter quality of mature trees grown in N-limited soils and under continuous exposure to elevated CO_2, changes at the ecosystem level.

Table 3. Litter decomposition of leaf material from Mediterranean species originating from elevated and ambient CO_2 levels at the Laiatico mineral CO_2 spring. (from Raiesi *et al.* 1997a,b; Raiesi, 1999). Standard deviations between brackets.

	Annual remaining mass[1] (%)	Cumulative CO_2-C respired[2] ($g.\ kg^{-1}$ C)	Cumulative N mineralized[3] ($g.\ kg^{-1}$ N)
Quercus cerris (n=2)			
Elevated CO_2 area	39.4 (0.2)	112 (3.0)	18.2 (0.5)
Ambient CO_2 area	31.7 (3.3)	117 (1.0)	17.3 (0.6)
Q. pubescens (n=2)			
Elevated CO_2 area	30.6 (2.9)	136 (7.0)	21.5 (1.1)
Ambient CO_2 area	30.0 (3.3)	172 (28)	20.5 (1.0)
S. aspera (n=3)			
Elevated CO_2 area	n.d.	53.2 (1.9)	-0.54 (0.35)
Ambient CO_2 area	n.d.	51.3 (3.2)	-1.08 (0.25)

[1] the incubation time 12 months
[2] the incubation time 90 days for *Quercus* species and 48 days for *S. aspera*
[3] the incubation time 125 days for *Quercus* species and 60 days for *S. aspera*

Effects of CO_2 enrichment on quality of litter apparently do not play a significant role in changing the carbon balance and SOM pools of Mediterranean woodland ecosystems containing typical oak-ash trees. This does not rule out the possibility that long-term elevated CO_2 will gradually increase the soil organic carbon pool through higher litter input caused by increased net primary production.

Table 4. The characteristics of soil organic matter of three soil layers in a Mediterranean forest exposed to elevated and ambient CO_2 at the Laiatico mineral CO_2 spring. (from Raiesi *et al.* 1999b,c).

	C (%)	N (%)	C/N (-)	C pool ($t. ha^{-1}$)	N pool ($g.m^{-2}$)	C decomposed[1] ($mg. g^{-1}$ soil)	N mineralized[2,3] ($mg. kg^{-1}$ soil)
F layer							
Elevated CO_2 area	43.3	1.80	24.2	12.2 a	50.4 a	9.07	154 a
Ambient CO_2 area	36.6	1.66	22.1	5.24 b	23.4 b	8.74	221 b
HA layer							
Elevated CO_2 area	34.4	1.58	21.7	24.4 a	112 a	5.72	134 a
Ambient CO_2 area	31.2	1.57	19.9	11.4 b	55.9 b	6.30	244 b
0-10 cm mineral soil							
Elevated CO_2 area	4.16	0.30	14.8	48.3	341	0.62	15.9
Ambient CO_2 area	4.87	0.27	19.4	57.9	323	0.60	7.28

[1] the incubation time 2 weeks
[2] the incubation time 4 weeks
[3] Forest floor = N immobilization, 0-10 cm layer = N mineralization

Species composition and SOM (C and N cycles)

Although elevated CO_2 had no significant impact on litter quality and decomposition, there were significant differences in litter quality and decomposition parameters between species (Tab. 1 and 3). *S. aspera* exhibited a better litter quality than the two oak species, while *Q. pubescens* litter had a better quality than *Q. cerris* litter. *Q. pubescens* litter decomposed faster than *Q. cerris* litter under controlled conditions, but not in the field. Why under field conditions plant leaf litter with a high quality does not necessarily decompose faster than plant leaf litter with a low quality may be due to specific micro-site characteristics (e.g. water, temperature), and high spatial micro-variability in some soil properties (e.g. soil microorganisms, root distribution, etc.).

This study suggests that differences in litter quality between plant species are greater than impacts of elevated CO_2 on litter quality and C and N cycling within a species. This implies that changes in plant species composition may be more important for soil C sequestration than direct effects of elevated CO_2 on the litter quality of a given species. Because within one ecosystem, plant species composition may change in response to CO_2 enrichment, the response of individual plant species can not be used to predict the response of plant communities. Change of species, through different responses of individual species (Bazzaz 1990; Field *et al.* 1992) may have a important influences through effects on litter turnover (Kemp *et al.* 1994) and thereby on C and N cycling. Such long-term feedbacks may eventually affect the structure and functioning and of ecosystems (Bazzaz 1990; Canadell *et al.* 1996).

Effect of elevated CO_2 on composition and dynamics of SOM

Over the past decade, many experiments have addressed the effects of elevated CO_2 on plant growth, but few on litter. Very few studies have paid attention to changes in SOM itself. Changes in native SOM are potentially important, since effects on the global C cycle, due to climate change, should be reflected in the soil where carbon resides for decades to centuries. Amthor (1995) suggested that natural CO_2 springs are the best available sites to examine the effects of long-term elevated CO_2 on soil C pool sizes and dynamics. The impact of elevated atmospheric CO_2 on N and C pools, and C and N turnover rates of SOM were determined by analyzing pool sizes of C and N of native soil organic matter at different distances from a CO_2 spring, as a function of a long-term CO_2 gradient. Results demonstrate that elevated CO_2 increased the C content and pool size of the forest floor (F +HA layers, Tab. 4). Such effects were not observed in the upper 10 cm of mineral soil (Tab. 4). A positive relationship between litter thickness and CO_2 concentration was also observed (data not shown); indicating that higher litter production may be expected with increasing atmospheric CO_2. The N content and the C/N ratios of the three soil layers, however, were not affected by elevated CO_2. Although the N content of the forest floor remained unaffected by elevated CO_2, N pool sizes at long-term elevated CO_2 sites were double those at ambient sites. This is not surprising, as the C/N ratio of plant materials reaching the forest floor, and their decomposition rates, remained unchanged under elevated CO_2 (Raiesi , 1998, 1999; Raiesi *et al.* 1999a, Tab. 1 and 3), and elevated CO_2 stimulates plant production in the long term (Jones *et al.* 1995; Hättenschwiler *et al.* 1997). Therefore, increased rates of carbon input must be associated with increased rates of net nitrogen accumulation. Similarly, Prior *et al.* (1997) found after

2 years that N pool size at 5-20 cm depth of a soil under wheat grown at 550 CO_2 ppm was significantly higher than that at ambient CO_2, but such a CO_2 effect was not observed at 0-5 cm of depth. However, the relative increase in N pools in the present study are much higher than those reported for experiments with wheat (Prior *et al.* 1997).

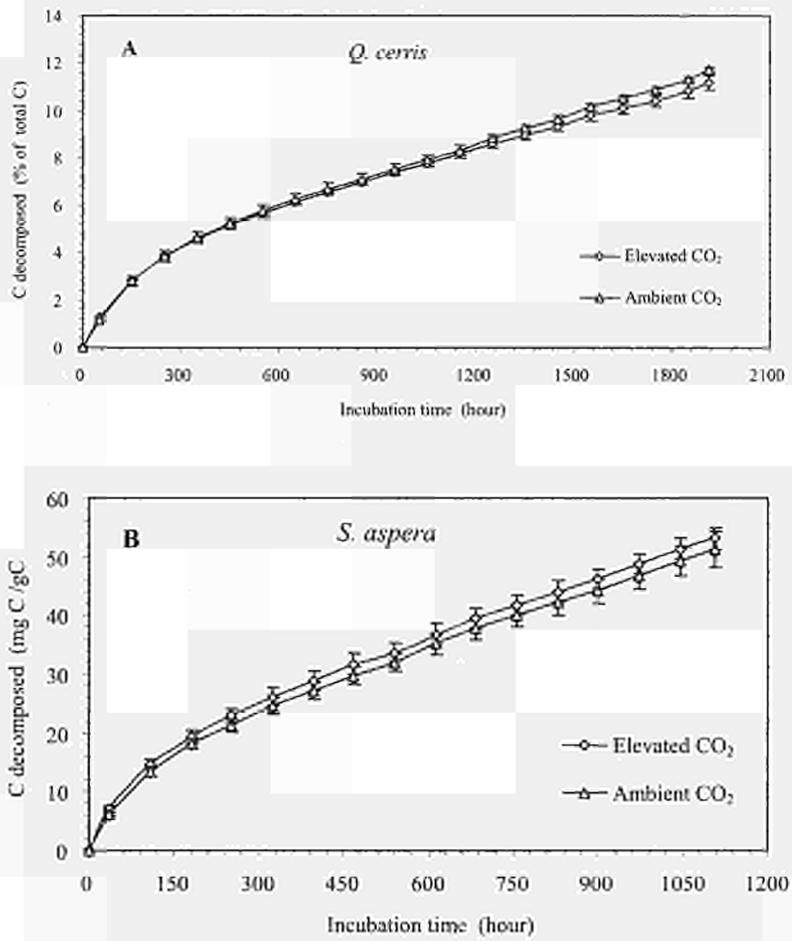
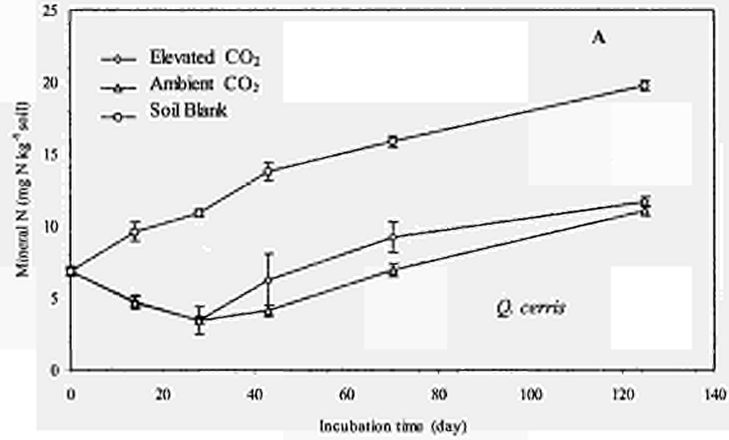


Figure 1. – C mineralization in *Q. cerris* (A) and *S. aspera* (B) litter produced under elevated and ambient CO_2 concentration, determined during a laboratory incubation at 20 °C (from Raiesi, 1999; Raiesi *et al.* 1999a).



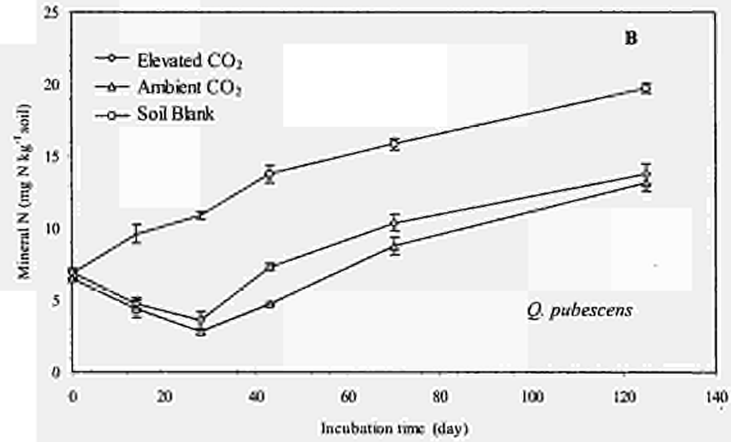


Figure 2. - N mineralization in *Q. cerris* (A) and *Q. pubescens* (B) litter produced under elevated and ambient CO_2 concentration, determined during a laboratory incubation at 20 °C for 125 days. Soil blank is the control soil without the addition of leaf litter (from Raiesi, 1998).

The Laiatico forest has been continuously exposed to elevated CO_2 for more than decades or centuries so that the remarkable increased N pools at elevated CO_2 is the result of a progressive accumulation of organic N over a long period of exposure. In contrast, Körner and Arnone (1992) observed that total N pools in the soil of an artificial tropical ecosystem were similar at both ambient and elevated CO_2, despite of an 38 % increase in litter production. Notwithstanding, the N pool in plant litter was 33% higher under elevated than ambient CO_2, suggesting the C/N ratio remains constant for both treatments.

Rates of soil C mineralization, estimated over two weeks under laboratory conditions, were not influenced by elevated CO_2, in accordance with the absence of a CO_2 effect on the N content and C/N ratios of soil organic matter. Therefore, the possible explanation for increased C pool size in the forest floor must be attributed to increased rates of litter input through enhanced Net Primary Production (NPP) at the elevated CO_2. Evidence to corroborate this has been reported by Jones *et al.* (1995) and Hättenschwiler *et al.* (1997), who observed stimulations in forest growth and production following exposure to long-term elevated CO_2. The rate of N immobilization in the forest floor (F plus HA layers), measured during 30-days incubation under controlled conditions, was lower at elevated than that at ambient CO_2, whereas the rate of N mineralization in mineral soil was unaffected. The decreased rate of N immobilization in the forest floor at elevated CO_2 is surprising because the chemical composition of soil organic matter and its decomposition rate remained unchanged as CO_2 increased. N mineralization in leaf plant litter grown at elevated CO_2 was higher at the initial stage of incubation, but this difference disappeared with time.

The absence of a CO_2 effect on litter quality, and consequently on litter decomposition, was generally reflected in the unchanged chemical composition and decomposition of soil organic matter. Although the decomposition of soil organic matter in a natural multi-species ecosystem is a complex process, and only a few factors that control SOM decomposition have been examined, we found no evidence for reduced SOM decomposition under increased CO_2.

In this study, we used SOM that was derived from plant materials continuously exposed to elevated CO_2, and considered the whole plant-soil system. The experiment included implicitly some plant-soil feed-backs, such as impacts of elevated CO_2 on below-ground C and processes, and thereby on soil C via the plant. Most experiments, which have reported reduced C mineralization under elevated CO_2 are either short-term or have used a soil-litter mixture that may not represent natural properties and processes as they occur in the field. Soil fauna are excluded from some studies conducted under controlled conditions, while it undoubtedly plays an important role in fragmentation of litter in the soil (Tian 1992; Coûteaux *et al.* 1991). We found that the rate of litter decomposition for the same litter type was not the same under laboratory and field conditions (Raiesi, 1998).

We deduct that the increase in the organic carbon pool of the forest floor, in the absence of an effect of elevated CO_2 on litter quality and decomposition, is explained by increased biomass production under elevated CO_2. Under elevated CO_2, soil N pools may also increase, but the rate of N immobilization in forest floor is lower than that at ambient CO_2. One reason to believe that sustained increases in plant growth under elevated CO_2 may be possible is the fact that N mineralization rates are stimulated by sustained CO_2 enrichment.

CONCLUSIONS

It is likely that changes in litter quality, litter decomposition and litter N mineralization rates, and consequently N availability, in response to higher levels of atmospheric CO_2

will not result in changes in the function of soil as a sink and (or) source of atmospheric CO_2. Evidence from a natural ecosystem, which has experienced long-term CO_2 enrichment, indicates a lack of positive or negative feedbacks from plant litter decomposition through atmospheric CO_2. At the same time, an increase in N pool-size and in soil N mineralization suggest that plant growth at elevated CO_2 may not be limited by low N availability in the soil. Higher C assimilation may lead to enhanced C accumulation in the soil, which may impose a negative feedback to the level of CO_2. in the atmosphere.

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