

## THE IMPACT OF ATMOSPHERIC CO<sub>2</sub> ENRICHMENT ON THE BIOGEOCHEMISTRY OF C AND N IN A MEDITERRANEAN FOREST ECOSYSTEM

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**ABSTRACT** - Elevated atmospheric CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> spring in Central Italy. Elevated CO<sub>2</sub> 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<sub>2</sub>, probably as a result of increased plant production. This suggests that elevated CO<sub>2</sub> increases the soil-sink of atmospheric CO<sub>2</sub>. Nitrogen immobilization in the forest floor was lower under elevated than ambient CO<sub>2</sub>, whereas N mineralization in the A horizon remained unaffected.

This study casts doubt on the common idea that elevated CO<sub>2</sub> changes litter quality, and thereby slows down decomposability of litter and N release, but strongly suggests that elevated CO<sub>2</sub> increases SOM pools via higher litter quantity through increased net primary production.

**Keywords:** Climate Change, litter quality and decomposition, Mediterranean ecosystems, mineral CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>"). The missing CO<sub>2</sub> may be trapped in soils and vegetation via CO<sub>2</sub> fertilization, forest regrowth in the northern hemisphere and atmospheric N deposition (Gifford 1994; Schimel 1995).

The rise in CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>. On the other hand, enhanced CO<sub>2</sub> 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<sub>2</sub> on SOM. To investigate these effects, long-term experiments are necessary. Natural CO<sub>2</sub> 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<sub>2</sub> on the dynamics of soil organic matter in a Mediterranean ecosystem which has been exposed to elevated CO<sub>2</sub> for an extended period. In this chapter, we present results from natural CO<sub>2</sub> springs where the effects of elevated CO<sub>2</sub> 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<sub>2</sub> are speculated upon. By obtaining soil data around CO<sub>2</sub> springs, we also attempt to answer several fundamental questions, such as “*Will elevated CO<sub>2</sub> affect quality and decomposability of litter of mature plants growing in N-limited ecosystems exposed to long-term elevated CO<sub>2</sub> for?*” and “*Are such CO<sub>2</sub> 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<sub>2</sub>O) 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<sub>2</sub> 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 in a CO<sub>2</sub> gradient from ambient (350 ppm) to about 600 ppm at the vent (Raiesi, 1998). Because factors other than atmospheric CO<sub>2</sub> concentration contribute to spatial differences in soil properties including SOM within the valley, a comparable transect (ambient CO<sub>2</sub>, 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<sub>2</sub> concentrations of c.550 ppm, and from a control area with 360 ppm CO<sub>2</sub>. 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<sub>2</sub> gradient of decreasing atmospheric CO<sub>2</sub> levels from the source to ambient (360 ppm) between 50 to 100 m from the vent (for a map of CO<sub>2</sub> 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 vent area, 9 in the control area) were sampled with a teathed auger (20 cm high and 8 cm  $\phi$ ). 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<sub>2</sub> concentration was measured. C and N decay rates were studied by tracking CO<sub>2</sub> 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<sub>2</sub> levels at the Laiatico mineral CO<sub>2</sub> spring. (from Raiesi *et al.* 1997a,b; Raiesi, 1998, 1999).

	Concentration (%)				Ratios (-)			
	N	Lignin	Cellulose	Polyph. <sup>1</sup>	C/N	Lignin/N	Cellulose/N	Polyph. <sup>1</sup> /N
<i>Quercus cerris</i> (n=2)								
Elevated CO <sub>2</sub> area	0.72	27.2	19.7	19.3	77.7	38.0	27.4	27.0
Ambient CO <sub>2</sub> area	0.76	26.8	20.6	20.5	73.6	35.0	26.9	26.6
<i>Q. pubescens</i> (n=2)								
Elevated CO <sub>2</sub> area	0.81	19.3	22.8	21.1	65.2	23.9	28.3	26.1
Ambient CO <sub>2</sub> area	0.84	18.5	21.4	19.7	63.2	22.9	25.8	24.0
<i>Smilax aspera</i> (n=3)								
Elevated CO <sub>2</sub> area	1.07	n.d.	n.d.	0.86	52.6	n.d.	n.d.	0.81
Ambient CO <sub>2</sub> area	1.01	n.d.	n.d.	0.82	56.1	n.d.	n.d.	0.81
<i>Q. ilex</i> (n=3)								
Elevated CO <sub>2</sub> area	0.75	n.d.	n.d.	n.d.	72.8	n.d.	n.d.	n.d.
Ambient CO <sub>2</sub> area	0.75	n.d.	n.d.	n.d.	72.2	n.d.	n.d.	n.d.
<i>Fraxinus ornus</i> (n=3)								
Elevated CO <sub>2</sub> area	0.75	n.d.	n.d.	n.d.	69.8	n.d.	n.d.	n.d.
Ambient CO <sub>2</sub> area	0.76	n.d.	n.d.	n.d.	69.2	n.d.	n.d.	n.d.

<sup>1</sup> Polyphenols; n.d., not determined.

## RESULTS AND DISCUSSION

### *Elevated CO<sub>2</sub> effect on litter chemistry and turnover*

We studied changes in litter chemistry of plants following exposure to long-term elevated CO<sub>2</sub> 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<sub>2</sub> were not significantly different from those from ambient CO<sub>2</sub> (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-senescent leaves of *S. aspera* were unaffected by CO<sub>2</sub> level (Tab. 2). Also the re-translocation of nitrogen during senescence (Table 2) appears unaffected by CO<sub>2</sub> level. This means that a decrease in efficiency of this translocation, as observed in other species (Arp and Berendse, 1993) is not found in *Smilax* exposed to long-term high CO<sub>2</sub> concentrations.

As expected from the litter quality data, rates of decomposition (measured with litter bags) in ambient and elevated CO<sub>2</sub> 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<sub>2</sub> (Tab. 3). Similarly, decomposition under laboratory conditions in *S. aspera* litter was unaffected by the CO<sub>2</sub> 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<sub>2</sub> than that at ambient CO<sub>2</sub> (Fig. 1), it was not affected by CO<sub>2</sub> in the long term (Tab. 3), again in accordance with the absence of a CO<sub>2</sub> impact on litter chemistry.

Results from long-term experiments around CO<sub>2</sub> springs provided evidence that increases in the atmospheric CO<sub>2</sub> concentration do not influence substrate quality, and therefore it is unlikely that rising CO<sub>2</sub> levels will affect C and N turnover rates of litter in terrestrial ecosystems. The lack of a CO<sub>2</sub>-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<sub>2</sub> concentrations around the Laiatico CO<sub>2</sub> spring.

CO <sub>2</sub> 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<sub>2</sub> 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<sub>2</sub>. 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<sub>2</sub>. Decreased efficiency of N-withdrawal under CO<sub>2</sub>-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<sub>2</sub>, but it seems that this mechanism can not explain unchanged litter quality with CO<sub>2</sub> enrichment.

Our long-term CO<sub>2</sub> studies cast doubt on the general concept that elevated CO<sub>2</sub> 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<sub>2</sub> effect on litter quality is still undecided, many field studies indicate that elevated CO<sub>2</sub> 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<sub>2</sub>, changes at the ecosystem level.

**Table 3.** Litter decomposition of leaf material from Mediterranean species originating from elevated and ambient CO<sub>2</sub> levels at the Laiatico mineral CO<sub>2</sub> spring. (from Raiesi *et al.* 1997a,b; Raiesi, 1999). Standard deviations between brackets.

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

<sup>1</sup> the incubation time 12 months

<sup>2</sup> the incubation time 90 days for *Quercus* species and 48 days for *S. aspera*

<sup>3</sup> the incubation time 125 days for *Quercus* species and 60 days for *S. aspera*

Effects of CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> at the Laiatico mineral CO<sub>2</sub> spring. (from Raiesi *et al.* 1999b,c).

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

<sup>1</sup> the incubation time 2 weeks

<sup>2</sup> the incubation time 4 weeks

<sup>3</sup> Forest floor = N immobilization, 0-10 cm layer = N mineralization

### *Species composition and SOM (C and N cycles)*

Although elevated CO<sub>2</sub> 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.).

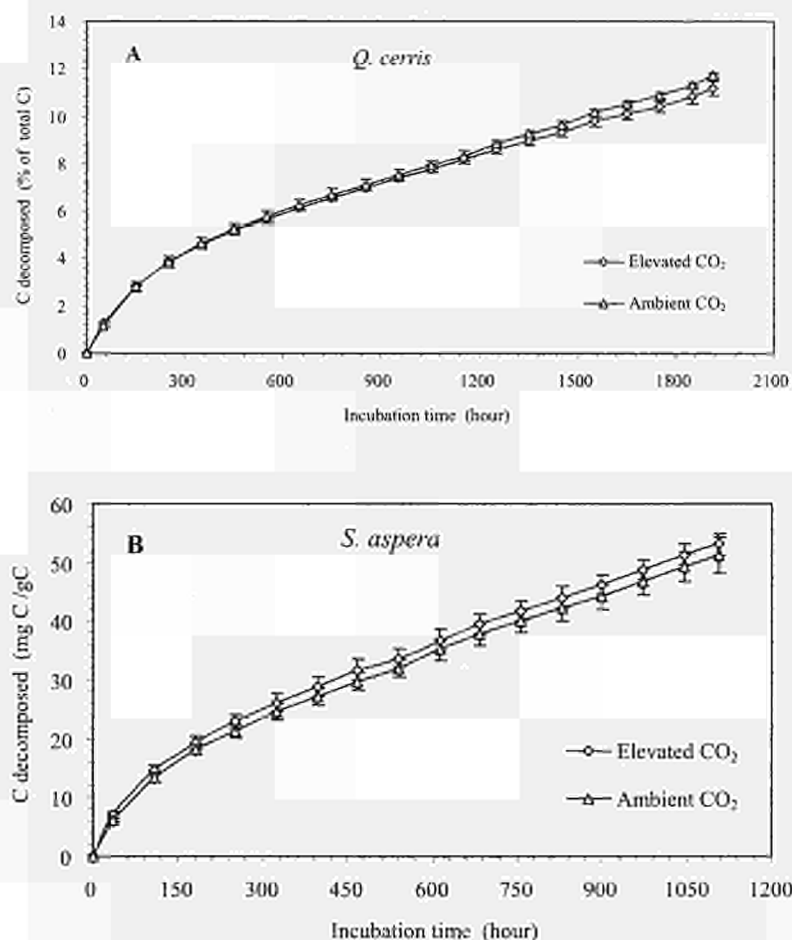
This study suggests that differences in litter quality between plant species are greater than impacts of elevated CO<sub>2</sub> on litter quality and C and N cycling within a species. This implies that changes in plant species composition may be more important for soil C sequestration than direct effects of elevated CO<sub>2</sub> on the litter quality of a given species. Because within one ecosystem, plant species composition may change in response to CO<sub>2</sub> 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<sub>2</sub> on composition and dynamics of SOM*

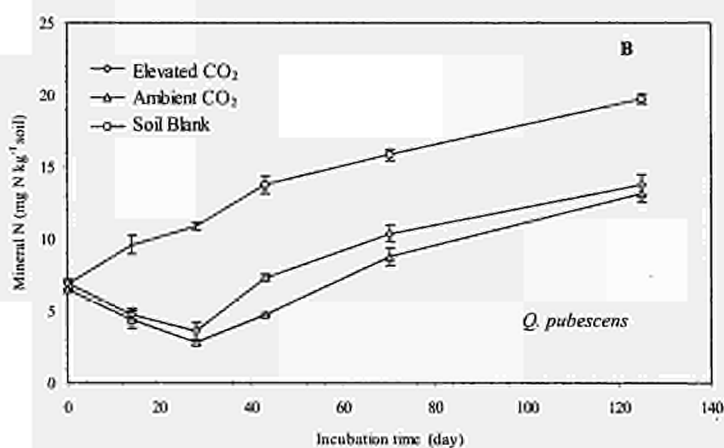
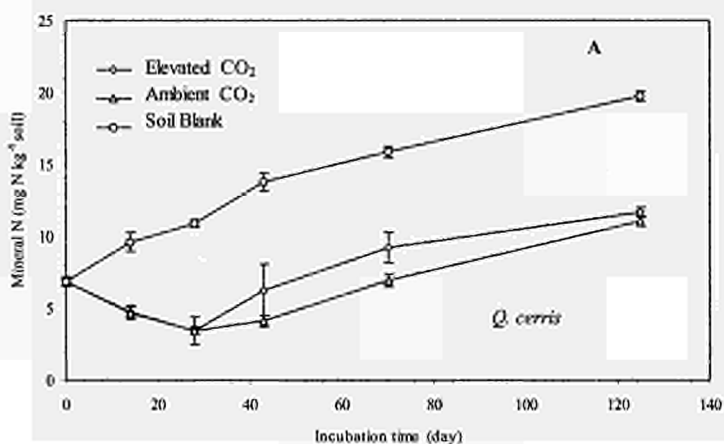
Over the past decade, many experiments have addressed the effects of elevated CO<sub>2</sub> on plant growth, but few on litter. Very few studies have paid attention to changes in SOM itself. Changes in native SOM are potentially important, since effects on the global C cycle, due to climate change, should be reflected in the soil where carbon resides for decades to centuries. Amthor (1995) suggested that natural CO<sub>2</sub> springs are the best available sites to examine the effects of long-term elevated CO<sub>2</sub> on soil C pool sizes and dynamics. The impact of elevated atmospheric CO<sub>2</sub> 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<sub>2</sub> spring, as a function of a long-term CO<sub>2</sub> gradient. Results demonstrate that elevated CO<sub>2</sub> 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<sub>2</sub> concentration was also observed (data not shown); indicating that higher litter production may be expected with increasing atmospheric CO<sub>2</sub>. The N content and the C/N ratios of the three soil layers, however, were not affected by elevated CO<sub>2</sub>. Although the N content of the forest floor remained unaffected by elevated CO<sub>2</sub>, N pool sizes at long-term elevated CO<sub>2</sub> 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<sub>2</sub> (Raiesi , 1998, 1999; Raiesi *et al.* 1999a, Tab. 1 and 3), and elevated CO<sub>2</sub> 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<sub>2</sub> ppm was significantly higher than that at ambient CO<sub>2</sub>, but such a CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> for more than decades or centuries so that the remarkable increased N pools at elevated CO<sub>2</sub> 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<sub>2</sub>, despite of an 38 % increase in litter

production. Notwithstanding, the N pool in plant litter was 33% higher under elevated than ambient CO<sub>2</sub>, 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<sub>2</sub>, in accordance with the absence of a CO<sub>2</sub> 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<sub>2</sub>. 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<sub>2</sub>. 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<sub>2</sub>, whereas the rate of N mineralization in mineral soil was unaffected. The decreased rate of N immobilization in the forest floor at elevated CO<sub>2</sub> is surprising because the chemical composition of soil organic matter and its decomposition rate remained unchanged as CO<sub>2</sub> increased. N mineralization in leaf plant litter grown at elevated CO<sub>2</sub> was higher at the initial stage of incubation, but this difference disappeared with time.

The absence of a CO<sub>2</sub> 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<sub>2</sub>.

In this study, we used SOM that was derived from plant materials continuously exposed to elevated CO<sub>2</sub>, and considered the whole plant-soil system. The experiment included implicitly some plant-soil feed-backs, such as impacts of elevated CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> on litter quality and decomposition, is explained by increased biomass production under elevated CO<sub>2</sub>. Under elevated CO<sub>2</sub>, soil N pools may also increase, but the rate of N immobilization in forest floor is lower than that at ambient CO<sub>2</sub>. One reason to believe that sustained increases in plant growth under elevated CO<sub>2</sub> may be possible is the fact that N mineralization rates are stimulated by sustained CO<sub>2</sub> 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<sub>2</sub>

will not result in changes in the function of soil as a sink and (or) source of atmospheric CO<sub>2</sub>. Evidence from a natural ecosystem, which has experienced long-term CO<sub>2</sub> enrichment, indicates a lack of positive or negative feedbacks from plant litter decomposition through atmospheric CO<sub>2</sub>. At the same time, an increase in N pool-size and in soil N mineralization suggest that plant growth at elevated CO<sub>2</sub> 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<sub>2</sub> in the atmosphere.

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