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The Response of Soil CO₂ Efflux under Trees Grown in Elevated Atmospheric CO₂: A Literature Review

By

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K e y w o r d s : Elevated CO₂, soil CO₂ efflux, soil respiration.

S u m m a r y

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As elevated atmospheric CO₂ concentrations typically result in larger root systems and increased litter production, also soil CO₂ efflux is expected to be enhanced in elevated CO₂. In a review of the related literature we did find a mean stimulation of soil CO₂ efflux of 37 %, but large differences occurred among different experiments. In some experiments, soil respiration was not or even negatively affected, despite significant increases in root biomass. We hypothesize that the lack of response of soil CO₂ efflux to increased CO₂ concentrations in those experiments was due to a retardation of soil organic matter and possibly also litter decomposition.

I n t r o d u c t i o n

Increasing levels of atmospheric CO₂ may significantly alter the terrestrial carbon (C) cycle. Next to the stimulation of photosynthesis and biomass production, one of the major effects of elevated atmospheric CO₂ concentrations (pCO₂) is the relative increase in C allocation to roots and mycorrhizae (CEULEMANS & al. 1999), resulting in larger root systems (ROGERS & al. 1994). The enhanced root biomass, and the stimulated delivery of labile C into the soil are likely to increase both the accumulation of C in the soil and the efflux of CO₂ from it.

Globally, the efflux of CO₂ from the soil (SCE) is roughly ten times larger than the anthropogenic emissions (SCHIMEL 1995). Thus, changes in root respiration and soil organic matter decomposition induced by elevated pCO₂ and

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rising temperatures might significantly influence the Earth's C cycle and the global climate. Here we present a literature review on the effects of elevated $p\text{CO}_2$ on SCE, and will try to explain the observations.

Results

Three significant observations were detected in the reported studies. Firstly, an increase in SCE was observed in response to CO_2 enrichment in most of the reported studies (Table 1), with an average stimulation of 37 %. However, several studies showed no stimulation, and even decreases in SCE were reported. Secondly, in all studies with multiple $p\text{CO}_2$ levels, the increase in $p\text{CO}_2$ from ambient to the first level always had a larger effect on SCE than the increase from that first level to a higher level (Table 1). Thirdly, the stimulatory effect changes considerably in time, with large intra- and interannual variability (data not shown).

Discussion

Elevated $p\text{CO}_2$ significantly stimulates root growth and root biomass (ROGERS & al. 1994), and rhizosphere respiration has been found to be very responsive to elevated $p\text{CO}_2$ (CHENG 1999, LIN & al. 1999). The observed decrease in SCE in some experiments is therefore an unexpected result. In the studies on *Fraxinus excelsior*, *Quercus petraea* and *Pinus sylvestris* by M. Broadmeadow (Table 1), root growth more than doubled (CROOKSHANKS & al. 1998), while soil respiration was unaltered or even decreased. In the experiment on *Fagus sylvatica* saplings (LE DANTEC & al. 1997), root biomass increased with 30 %, but SCE nevertheless decreased by 10 % (Table 1). Furthermore, also in several experiments where SCE did significantly increase, this stimulation was still small compared to the effect on root biomass. In the study on *Pinus sylvestris* (JANSSENS & al. 1998), e.g., SCE increased significantly by 25 %, but fine root biomass increased by 135 %.

Part of this discrepancy is related to the fact that root respiration is only a fraction of total SCE, and therefore a doubling of root biomass will not lead to a doubling of SCE. In addition, biomass produced under high $p\text{CO}_2$ is usually characterised by reduced N concentrations (COTRUFO & al. 1998), possibly resulting in a reduction of specific root respiration rates (RYAN & al. 1996). Although these arguments may explain why the stimulation of SCE is smaller than the stimulation of rhizosphere respiration, it cannot explain the reported decreases. Thus, the negative and small responses suggest that (in some cases) elevated $p\text{CO}_2$ may negatively affect decomposition of litter or soil organic matter (SOM).

It has been hypothesised that the reduced litter N concentrations would retard their decomposition in the initial stages. Since most of the studies in Table 1 were short-term, the deposited litter may still have been in these initial stages of decomposition, and thus decomposing at a slower rate. This may have contributed

to the moderate response of SCE observed in some studies. However, because of the relatively small litter production in these young ecosystems and the long turnover periods of the produced litter, it seems unlikely that the potentially retarded litter decomposition rates significantly reduced the response of SCE. We therefore suggest that, under certain conditions, retarded SOM decomposition rates can offset the increase in rhizosphere respiration. Reduced rates of SOM decomposition have indeed been found in some studies (although not in many others), but the conditions under which this reduction occurs remain unclear (CHENG 1999). The effects of exudation and soil nutrient status on the mineralisation of SOM, and the competition for nutrients between plants and microbes appear to be of major importance.

Table 1. Responses of soil CO₂ efflux under CO₂-enriched trees. For each study, also growth conditions, pCO₂ and the reference are given. (OTC's = open top chambers; GH = greenhouse, A = ambient). We calculated means for studies where results were reported separately for different measurement periods.

Species	Conditions	pCO ₂	Mean E/A	Reference
<i>Acer rubrum</i>	OTC's	A, 700	1.27	(EDWARDS & NORBY 1999)
<i>Acer saccharum</i>	OTC's	A, 700	1.05	(EDWARDS & NORBY 1999)
<i>Betula pendula</i>	OTC's	A, +350	1.95	(REY & al. 1997)
<i>Castanea sativa</i>	GH	A, 700	1.53	(ROUHIER & al. 1996)
<i>Fagus sylvatica</i> seedlings	Open-sided growth chambers	A, +350	2.71 (high N) 1.41 (low N)	(LE DANTEC & al. 1997)
<i>Fagus sylvatica</i> saplings	Open-sided growth chambers	A, +350	0.90	(LE DANTEC & al. 1997)
<i>Fraxinus excelsior</i>	OTC's	A, +350	1.10	(BROADMEADOW unpubl.)
<i>Liriodendron tulipifera</i>	OTC's	A, 500, 750	1.25 1.22	(NORBY & al. 1992)
Macchia vegetation	OTC's	A, +350	1.13	(DE ANGELIS & al. unpubl.)
<i>Picea abies</i>	Microcosms	280, 420, 560	1.13 1.18	(HÄTTENSCHWILER & KÖRNER 1997)
<i>Pinus ponderosa</i>	OTC's, low N	A, 525, 700	1.57 1.93	(JOHNSON & al. 1994)
<i>Pinus ponderosa</i>	OTC's, high N	A, 525, 700	1.44 1.33	(JOHNSON & al. 1994)
<i>Pinus ponderosa</i>	OTC's	A, 525, 700	1.67 1.35	(VOSE & al. 1997)
<i>Pinus sylvestris</i>	OTC's	A, +350	1.25	(JANSSENS & al. 1998)
<i>Pinus sylvestris</i>	OTC's	A, +350	0.98	(BROADMEADOW unpubl.)
<i>Pinus sylvestris</i>	OTC's	A, 525	1.54	(PAJARI 1995)
<i>Pseudotsuga menziesii</i>	Microcosms	A, +200	1.15	(LIN & al. 1999)
<i>Quercus alba</i>	OTC's	A, 500, 750	1.22 1.37	(NORBY 1996)
<i>Quercus petraea</i>	OTC's	A, +350	1.03	(BROADMEADOW unpubl.)
Tropical forest	Microcosms	A, 610	1.89	(KÖRNER & ARNONE 1992)

DE ANGELIS & CHIGWEREWE measured SCE at three-weekly intervals for three years in a mature Mediterranean macchia vegetation growing in OTC's (DE ANGELIS & SCARASCIA-MUGNOZZA 1998). These authors observed a small and non-significant increase in the first and third year, whereas in the second year they found a large stimulation. The effect of pCO_2 on SCE fluctuated strongly and negative responses were observed even within the second year. These temporal fluctuations may be an important source of error in studies based on few measurements, and may have contributed to the variability among these studies.

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