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Leaf Litter Under Changing Climate: Will Increasing Levels of CO_2 and O_3 Affect Decomposition and Nutrient Cycling Processes?

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ABSTRACT

In this manuscript we review existing information about CO_2 and O_3 effects on leaf litter as well as discuss the potential impacts of climate change on decomposition processes and tree nutrition. So far field studies show that the average response to elevated CO_2 is increased litter production and increased litter C:N-ratios, the latter response being more prominent in deciduous than in coniferous trees. The few O_3 studies indicate that O_3 stress may decrease some nutrient concentrations, but O_3 effects on carbon-based compounds are more ambiguous. In general, field incubation studies show only some small or inconsistent CO_2- and O_3-induced changes in litter mass loss rates. On the other hand, recent long-term studies indicate that there are some CO_2 and O_3 effects on microbial functioning in the soil (e.g. CO_2 stimulates and O_3 dampens it), although the onset of these microbial responses may take years. Nonetheless, at the moment there is no consistent evidence of CO_2-induced and microbe-mediated progressive nitrogen limitation in temperate forests. Elevated O_3 effects on nutrient cycling are far less studied, and also more information about long-term CO_2 and O_3 effects on decomposition and nutrient cycling in boreal forests is still needed. Furthermore, some results indicate that the combined effects cannot be predicted on the basis of single exposures and therefore, the effects of increasing CO_2 and O_3 on decomposition and nutrient cycling processes must be studied in combination.

Keywords: carbon, carbon dioxide, coniferous trees, deciduous trees, decomposition, leaf litter, lignin, microbial activity, nitrogen, ozone, phenolic compounds, soil food web

Abbreviations: **B**, boron; **C**, carbon, **Ca**, calcium; **CO_2**, carbon dioxide; **Cu**, copper; **FACE**, free-air carbon dioxide enrichment; **Fe**, iron; **K**, potassium; **LMWP**, low-molecular-weight phenolic; **Mg**, magnesium; **Mn**, manganese; **N**, nitrogen; **NH^{+4}**, ammonium; **NO_x**, nitrogen oxides; **NUE**, nitrogen use efficiency; **O_3**, ozone, **OTC**, open-top chamber; **P**, phosphorus; **PNL**, progressive nitrogen limitation; **ppb**, parts per billion, nl l^{-1}; **ppm**, parts per million, µl l^{-1}; **S**, sulphur; **SOM**, soil organic matter; **VOC**, volatile organic compound; **Zn**, zinc

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INTRODUCTION

Before the Industrial Revolution, the atmospheric CO_2 level was around 280 ppm, whereas in 2005 the CO_2 concentrations in the surface layer of atmosphere had reached a level of 379 ppm (IPCC 2007a), which represents a global increase of 35% from the pre-industrial situation. With current climate change mitigation policies, global surface CO_2 levels will continue to grow over the next few decades, and are expected to be doubled from the pre-industrial level by the year 2100 mainly because of burning of fossil fuels and land-use change (Keeling *et al*. 1995; IPCC 2007b). Simultaneously, the annual mean concentrations of O_3 have reached levels of 20 to 50 ppb worldwide (Carter and La Rovere 2001; Vingarzan 2004). This increase of surface levels of O_3 is expected to continue, and some scenarios suggest that the average increase of surface O_3 levels will be 8-10% at the global level during the next decade (Collins *et al*. 2000; Jonson *et al*. 2001; IPCC 2001; Vingarzan 2004). The primary reason behind the increased O_3 levels in the troposphere is the human activity and its effect on ozone precursors (i.e., O_3 is generated from NO_x and VOCs in the presence of sunlight; Fowler *et al*. 1998). In particular global emissions of NO_x have increased due to energy production and transport during the past three decades (Vingarzan 2004; Ashmore 2005).

In the near future forest ecosystems will be increasingly exposed to the joint effects of CO_2 and O_3. Although there

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Invited Review

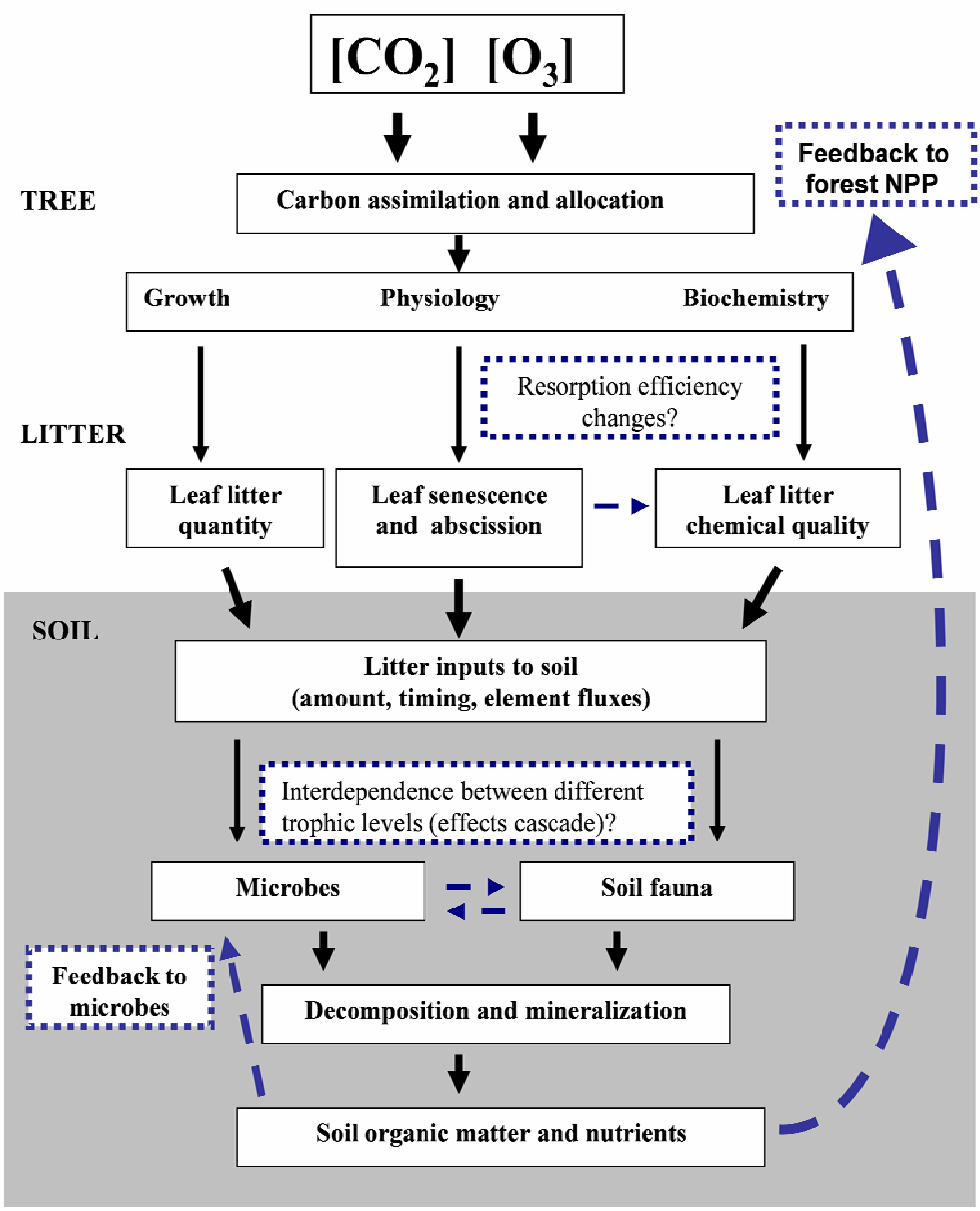

Fig. 1 Conceptual model of potential CO_2 and O_3 effects on trees and leaf litter, including links to soil food web, decomposition and mineralization processes and net primary productivity (NPP). See text for details.

are already a substantial number of CO_2 and O_3 studies about tree growth and physiology (Andersen 2003; Ainsworth and Long 2005; Grantz *et al*. 2006), the effects of these two greenhouse gases on decomposition and thereby nutrient cycling is still inadequately understood. The effects of elevated CO_2 and O_3 on decomposition are considered to be mainly indirect (**Fig. 1**). Hence, neither of these gases penetrates the soil extensively (Turner *et al*. 1973; Blum and Tingey 1977; Lamborg *et al*. 1983), but instead both CO_2 and O_3 first affect the tree C assimilation and C allocation within the tree, thereby influencing tree growth, physiology and biochemistry (Andersen 2003; Ainsworth and Long 2005). In theory, CO_2- and O_3-induced changes in green foliage are considered to be transmitted to leaf litter quantity and quality, and therefore changes in decomposition and element cycling processes as well as in net primary production (NPP) have been suggested to occur (Strain and Bazzaz 1983; Andersen 2003). However, it has been also suggested that elevated CO_2 and O_3 levels may alter leaf senescence and abscission processes (Norby *et al*. 2001; Andersen 2003) and thereby alter timing of leaf litter inputs to the soil and nutrient resorption efficiency in the foliage. If nutrient resorption efficiency changes under elevated CO_2 and O_3, litter chemistry responses may be masked or partly differ from those observed in green foliage. On the other hand, CO_2 and O_3 may affect decomposition via altered soil environment. For instance, CO_2- or O_3-induced changes in NPP can result in changed litter inputs and element fluxes to the soil or altered soil moisture conditions, and thereby affect soil biota functioning and biomass. Soil microbial responses to altered C fluxes may depend on the pre-existing soil organic matter pools and nutrient availability (Hu *et al*. 1999; Zak *et al*. 2000a, 2000b) in soil. If there are CO_2- and O_3-induced changes in the soil microbial biomass or community composition, these effects may also be propagated through higher levels of the soil food web, as there is a high degree of interdependence among different trophic levels (Coûteaux and Bolger 2000; Andersen 2003). Finally, although beyond the scope of this review, increasing levels of CO_2 and O_3 in the troposphere are leading to the global warming (IPCC 2007a) and in the future this climate warming may alter the decomposition processes substantially.

Since the CO_2 and O_3 effects on plant growth and physiology have been usually opposite, it has been widely suggested that elevated CO_2 may protect trees from O_3 stress (Volin *et al*. 1998; Podila *et al*. 2001). However, it is difficult to predict ecosystem-level responses because the CO_2 responsiveness and O_3 sensitivity varies widely both within

and among tree species (Karnosky *et al*. 2003). Largely based on above-ground tree growth and physiology data, responses to combined exposure are variable and can range from positive to negative or no net effect thus making predicting even more difficult. Because the above-ground responses to CO_2 and O_3 may partly differ in magnitude or direction from those of below-ground, they do not necessarily reliably describe the possible response patterns in the decomposition processes.

In this chapter we review existing literature about elevated CO_2 and O_3 effects on decomposition and nutrient cycling. We focus on leaf litter studies made with various deciduous and coniferous tree species. A majority of the leaf litter studies have been single-factorial studies, i.e., either CO_2 or O_3 studies, and mainly concentrated on leaf litter chemical quality changes and subsequent decomposition after the CO_2 and O_3 exposures. In litter studies the most commonly measured variables include N, C and lignin concentrations, C:N-ratios, and mass loss of leaf litter. However, recently there have been also some published results about leaf litter decomposition under elevated gas levels, and a few studies have included the CO_2 and O_3 effects on soil biota (microbes and soil fauna) or element (C and nutrient) cycling in the soil.

EFFECTS OF ELEVATED CO_2 ALONE

Litter quantity and quality responses

Elevated [CO_2] has usually enhanced leaf litter production in trees (Norby *et al*. 2002; Liu *et al*. 2005), but there are also results which indicate no CO_2-induced increases (Cotrufo *et al*. 2005) and species- or genotype-dependent responses to CO_2 in leaf litter production (Finzi *et al.* 2002; Riikonen *et al*. 2004). Recently Hungate *et al.* (2006) reported that in a scrub oak stand litterfall production increased initially under elevated CO_2 treatment, but after the fifth exposure season this CO_2 stimulation declined. The authors (Hungate *et al.* 2006) suggested that the declining trend was due to the accumulation of N in the surface soil organic matter, which caused the apparent restriction of plant available N and reduced the positive litter production response to CO_2 over time. On the other hand, two long-term FACE studies have shown sustained CO_2 stimulation of litter production even after six years of CO_2 exposure (Finzi *et al.* 2006; Norby and Iversen 2006). In a sweetgum stand the CO_2-induced litter production was sustained by enhanced N uptake (Norby and Iversen 2006), while in a loblolly pine dominated stand (Finzi *et al*. 2006), CO_2-exposed trees increased both their N uptake and nitrogen use efficiency and thereby sustained the increased litter production.

So far litter studies have shown either delay, enhancement or no change in leaf senescence or abscission rates (Mcconnaughay *et al*. 1996; Li *et al*. 2000; Johnson *et al*. 2001; Riikonen *et al*. 2004; Tricker *et al*. 2004; Cotrufo *et al*. 2005), and neither there is clear evidence of CO_2-induced changes in N resorption in trees (Norby *et al*. 2000; Finzi *et al*. 2001; Lindroth *et al*. 2001; Norby *et al*. 2001; Finzi and Schlesinger 2002; Kasurinen *et al*. 2006). Thus, the generally seen CO_2-induced decreases in N and thereby increases in C:N-ratio of green foliage should be carried over to the litter quality (Gifford *et al.* 2000; Norby *et al*. 2001). Support for this statement comes from several pot and field studies where the average CO_2 response is a decrease in N concentrations and an increase in leaf litter C:N-ratio in various tree species (Cotrufo and Ineson 1996; Cotrufo *et al*. 1998a; Gifford *et al*. 2000; Norby *et al*. 2001; **Table 1**). When we calculated the average response ratios for tree litter N across individual open-top chamber (OTC) and free-air CO_2 enrichment (FACE) experiments, the average CO_2 response for litter N was stronger (12% lower N in CO_2 treatments across the studies, **Table 1**) than that observed previously in the meta-analysis of Norby *et al*. 2001 (7% lower N in CO_2 treatments across the studies). The discrepancy between the above results can be explained by the fact that Norby *et al*. (2001) included data also from experiments where the leaf litter N responses of non-woody species were investigated and did not separate growth chamber and pot seedling studies in the compilation, whereas we used only data from OTC- and FACE-experiments conducted with soil-growing trees.

In the meta-analysis of Norby *et al*. (2001) the N response in individual studies was rarely statistically significant, whereas in our comparison (**Table 1**) some individual studies showed clear CO_2-induced decreases in litter N concentrations (e.g. De Angelis 2000; King *et al*. 2001b; Parsons *et al*. 2004; Cotrufo *et al*. 2005; Kasurinen *et al*. 2006). However, sometimes these N reductions were observed only after the first exposure season (Norby *et al*. 2000) or were tree community-dependent (Liu *et al*. 2005). In our data compilation (**Table 1**) the average trend is increasing C:N-ratio (19% higher C:N-ratio in elevated CO_2) across various CO_2 studies with soil-growing trees. Earlier Norby *et al*. (2001) concluded that the change in C:N-ratio in soil-growing trees may not necessarily be as large and universal as previously predicted on the basis of short-term pot experiments, and also N nutrition status may modify responses to CO_2 (Gifford *et al*. 2000). For instance, King *et al*. (2001a) observed a clear CO_2-induced increase in C:N-ratios of trembling aspen litter only under low soil N availability, whereas N addition to soil removed the CO_2 effect on litter C:N-ratio. On the other hand, in another study with sugar maple trees (King *et al.* 2001b), the initial litter C:N-ratios decreased under high CO_2 + low N and increased under high CO_2+high N treatment (**Table 1**). In addition, Hättenschwiler and Bretscher (2001) observed that both the soil type and N deposition can modify litter N responses to CO_2. Thus, at the calcareous soil site high CO_2 resulted in clear decreases in beech leaf N concentration under both high and low soil N, although this negative CO_2 response was somewhat bigger in the low N treatment (**Table 1**). At the acidic site, instead, high CO_2 clearly decreased beech litter N under high N deposition only, whereas under low N deposition the CO_2 effect on N was negligible (**Table 1**). A recent meta-analysis of green foliage data also indicates that N response to CO_2 may be more prominent in deciduous than in coniferous trees (Zvereva and Kozlov 2006). In our summary (**Table 1**), all the significant leaf litter N reductions were also observed in deciduous tree species. However, there is still a lack of OTC- and FACE- experiments where naturally abscised needle litter has been investigated.

In contrast to leaf litter N concentrations (Norby *et al*. 2001; **Table 1**), litter P concentrations have generally increased under elevated CO_2. In our data compilation (**Table 1**) the average P response was +12% across CO_2 studies, but usually these CO_2-induced increases were not statistically significant in the individual experiments (**Table 1**). Finzi *et al.* (2001) observed that in a loblolly pine dominated stand the P response to CO_2 differed between the green foliage (no CO_2-induced increase in P) and leaf litter (CO_2-induced increase in P) and especially in red bud trees. However, when Finzi *et al.* (2001) calculated P resorption proficiency in red bud trees, they noticed that it was only transiently decreased due to CO_2 enrichment (i.e. CO_2 effect on P resorption was significant only after the first exposure season and then disappeared). In our study with soil-growing birch trees the P concentration response to CO_2 was similar between green foliage and leaf litter indicating that the P resorption proficiency was not significantly altered over the three-year CO_2 exposure (Kasurinen *et al*. 2006; **Table 1**). The reason for the increased P concentrations both in green foliage and leaf litter (Kasurinen *et al*. 2006) could be that in contrast to N, plant P requirement for photosynthetic machinery is not necessarily down-regulated (Conroy and Hocking 1993), but instead, the stimulation of photosynthesis may increase the P requirement for the phosphorylated photosynthetic intermediates and intercellular transport under elevated CO_2 (Gifford *et al*. 2000). Liu *et al*. (2007) also reported statistically significant increases in litter P concentrations under elevated CO_2 in aspen and aspen-birch

Table 1 Summary of CO_2 effects on leaf litter chemistry. Treatment effect % = (the CO_2 treatment average response minus the control treatment average response divided by the control treatment average response) × 100. Negative values indicate decrease and positive values increase in chemical concentration or C:N-ratios, and 0 denotes for no change. Bolded values indicate an average response to CO_2 treatment across the individual experiments. Symbols: * = a significant CO_2 effect ($P \leq 0.1$), ** = tree community-dependent CO_2 response, (*) = CO_2 effect transient. Only data from OTC- and FACE-studies with soil-growing trees and naturally abscised leaf litter was included. Abbreviation nd = not determined.

Tree species/community	N	P	C:N-ratio	Lignin	Condensed tannins	Reference
Acer rubrum (ambient temperature)	-18(*)	nd	nd	nd	nd	Norby *et al*. 2000[1]
Acer rubrum (elevated temperature)	-10(*)	nd	nd	nd	nd	Norby *et al*. 2000[1]
A. rubrum	-8	+26	nd	-3	nd	Finzi *et al.* 2001[1]
A. rubrum	-4	nd	nd	+2	nd	Finzi and Schlesinger 2002[1]
A. saccharum (ambient temperature)	-7(*)	nd	nd	nd	nd	Norby *et al.* 2000[1]
A. saccharum (elevated temperature)	-12(*)	nd	nd	nd	nd	Norby *et al.* 2000[1]
A. saccharum (low N)	-10*	nd	-7*	nd	+31*	King *et al.* 2001b
A. saccharum (high N)	-18*	nd	+26*	nd	+40*	King *et al.* 2001b
Betula papyrifera	-31*	nd	+44*	+5	+64*	Parsons *et al*. 2004
B. pendula	-11*	+18*	+12*	+4*	+23*	Kasurinen *et al.* 2006, 2007[2]
B. papyrifera-Populus tremuloides	-18*	+14*	+20*	+6	+63**	Liu *et al.* 2005, 2007
Cornus florida	-26	+6	nd	-19	nd	Finzi *et al*. 2001[1]
C. florida	-13	nd	nd	0	nd	Finzi and Schlesinger 2002[1]
Cercis canadensis	0	+38	nd	-6	nd	Finzi *et al*. 2001[1]
C. canadensis	-14	nd	nd	+1	nd	Finzi and Schlesinger 2002[1]
Fagus sylvatica (acidic soil+low N)	-2	nd	nd	+3	nd	Hättenschwiler and Bretscher 2001
F. sylvatica (calcareous soil+low N)	-21*	nd	nd	+4	nd	Hättenschwiler and Bretscher 2001
Fagus sylvatica (acidic soil+high N)	-15*	nd	nd	+8*	nd	Hättenschwiler and Bretscher 2001
F. sylvatica (calcareous soil+high N)	-11*	nd	nd	0	nd	Hättenschwiler and Bretscher 2001
Liquidampar styraciflua	-8	+19	nd	+8	nd	Finzi *et al.* 2001[1]
L. styraciflua	-15	nd	nd	+3	nd	Finzi and Schlesinger 2002[1]
Pinus taeda	+3	+16	nd	-1	nd	Finzi *et al.* 2001[1]
P. taeda	0	nd	nd	+5	nd	Finzi and Schlesinger 2002[1]
P. sylvestris	-7	-11	nd	nd	nd	Kainulainen *et al.* 2003
Populus alba	-5*	nd	+7*	-7	nd	Cotrufo *et al.* 2005
P. × *euramericana*	-36*	nd	+45*	-4	nd	Cotrufo *et al*. 2005
P. nigra	-23*	nd	+29*	+2	nd	Cotrufo *et al.* 2005
P. tremuloides	-14*	+5*	+13*	+37	-18**	Liu *et al*. 2005, 2007
Quercus ilex	-12*	-13	+21*	+19*	nd	de Angelis *et al*. 2000[1]
Q. myrtifolia (Exp. 1)	0	nd	+1	-8	+12	Hall *et al.* 2006
Q. myrtifolia (Exp. 2)	-2	nd	+2	+30*	+2	Hall *et al*. 2006
Average response (n = 8 - 31)	**-12**	**+12**	**+18**	**+4**	**+27**	

communities. They (Liu *et al.* 2007) suggested that the CO_2-induced increase in P concentrations of leaf litter could be due to a concurrent increase in cuticular wax production (Percy *et al.* 2002), which could have reduced P leaching from the leaves under elevated CO_2.

The impact of CO_2 enrichment on other nutrients than N and P are far less studied. Cotrufo *et al*. (1998a) reviewed pot seedling and growth chamber studies and did not find any clear CO_2 responses in tree litter K, Ca, Mg, Mn and Fe concentrations. The few field experiments with soil-growing trees have not either been able to provide evidence of strong or consistent CO_2 effects on other nutrients. For instance, Kainulainen *et al*. (2003) did not find any CO_2 treatment effect on K, Ca and Mg concentrations of Scots pine needle litter after a three-year CO_2 exposure. In our study with two silver birch clones S concentration decreased under elevated CO_2 levels, but the other analysed nutrients (Ca, Mg, Mn, Fe, Zn, Cu, B) did not show any consistent change or the CO_2-induced changes were largely genotype-dependent (e.g. decrease in K concentrations) (Kasurinen *et al*. 2006). Liu *et al*. (2007) observed that elevated CO_2 marginally significantly increased litter K and S concentrations and significantly decreased B concentrations in both aspen and aspen-birch communities while litter Mn responses to CO_2 were community-dependent.

In addition to CO_2-induced changes in the amount of total C entering the soil, the changes in litter C compound composition (i.e. changes in C quality) may also play a significant role in the subsequent decomposition processes (Horner *et al*. 1988; Zak *et al*. 1993; Hättenschwiler and Vitousek 2000; Zak *et al*. 2000a, 2000b). The carbon-nutrient hypothesis (Bryant *et al*. 1983) and its extension, the growth-differentiation balance hypothesis (Herms and Mattson 1992), predict that changes in source-sink relationship could lead to variations in the relative partitioning of carbon to growth, total non-structural carbohydrates and carbon-based secondary and structural compounds. Thus, under elevated [CO_2] carbon source may be higher than carbon sink, and excess carbon could lead to the over-investment of non-structural carbohydrates and secondary or structural C compounds (Koricheva *et al*. 1998; Peñuelas and Estiarte 1998; Peltonen *et al*. 2005), especially under low soil N conditions (Lambers 1993). However, the magnitude of this CO_2 response has been observed to vary between different exposure systems (Norby *et al*. 2001) and C compound groups (Zvereva and Kozlov 2006). For instance, in pot seedling studies leaf litter lignin concentrations usually clearly increased under elevated CO_2, but OTC- or FACE-studies with soil-growing trees do not uniformly support these early findings (Norby *et al*. 2001, **Table 1**). In fact, only a few OTC studies have reported statistically significant increases in lignin concentrations under elevated CO_2 (DeAngelis *et al*. 2000; Hall *et al*. 2006; Kasurinen *et al*. 2006). When we summarized condensed tannin data across the OTC- and FACE-experiments (only tree litter results were used), we observed that in contrast to lignin, the average CO_2 response was relatively high (27% increase on average) and that in most individual studies this CO_2 effect was also statistically significant (**Table 1**). Furthermore, our OTC experiment indicated that elevated CO_2 has the potential to increase total phenolics and cellulose concentrations in silver birch litter (Kasurinen *et al*. 2006, 2007), while other studies with various tree species show no CO_2-induced increases in phenolics (Kainulainen *et al*. 2003) or cellulose concentrations (Liu *et al*. 2005; Hall *et al*. 2006). Of less studied terpene compounds, α- and β-pinene has

been observed to increase due to CO_2 enrichment, whereas total monoterpenes have not shown any clear CO_2-induced increase in Scots pine litter (Kainulainen *et al*. 2003).

Decomposition and soil food web responses

Results to date from litter decomposition studies have been variable and inconclusive (O'Neill and Norby 1996; Cotrufo *et al*. 1998a, 1998b; Coûteaux *et al*. 1999; Norby *et al*. 2001; **Table 2**). Laboratory studies with CO_2-exposed material have shown substantial rate retarding effects of CO_2 on the subsequent litter decomposition, but field litter incubations usually have not been able to confirm these early findings (O'Neill and Norby 1996; Norby *et al*. 2001). Thus, with few exceptions, a majority of the field incubation studies conducted under ambient CO_2 conditions have not detected any significant or consistent CO_2-induced changes in the decomposition rates (O'Neill and Norby 1996; Norby *et al*. 2001; **Table 2**). In our three-year study with silver birch, the negative CO_2 effect on decomposition was genotype-dependent and transient as elevated CO_2 decreased the subsequent decomposition in one birch clone only after the first and second exposure season (Kasurinen *et al*. 2006). On the other hand, some field incubation studies indicate that the CO_2 environment itself may modify the leaf litter decomposition responses significantly (**Table 2**). Parsons *et al*. (2004) reported that under ambient CO_2 plots, paper birch leaf litter produced in high CO_2 treatments decomposed slower than that produced in ambient CO_2 treatments, whereas in elevated CO_2 plots, the CO_2 enrichment itself during the decomposition process reinforced the negative effects of CO_2 on mass loss even further. Hall *et al*. (2006) observed that high CO_2 environment itself enhanced scrub oak litter decomposition, but the litter origin (i.e. whether it was produced under ambient or elevated CO_2 level) did not affect the decomposition rates in ambient or elevated CO_2 environment. Cotrufo *et al*. (2005) found that independent of the poplar species, litter generated under elevated CO_2 had slightly lower mass loss rates than litter produced under ambient CO_2, whereas in high CO_2 environment the decomposition rates of leaf litter of two poplar species were enhanced regardless of the litter origin (i.e. whether it was from ambient or elevated CO_2 plot). Thus, basically Cotrufo *et al*. (2005) observed that under ambient CO_2 environment CO_2-induced changes in leaf litter quality governed the decomposition rates, whereas in elevated CO_2 plots the CO_2-induced changes in soil environment itself may have controlled the litter disappearance. However, the authors (Cotrufo *et al*. 2005) did not give any specific causative mechanism for the latter observation, e.g., whether the increased decomposition in CO_2 plots was due to enhanced microbial activity or some other factor. In a loblolly pine-dominated stand, leaf litter decomposition of five different tree species (**Table 2**) was not significantly affected by the CO_2 exposure during the litter decomposition (Finzi *et al*. 2001; Finzi and Schelesinger 2002).

The role of soil animals in the actual decomposition process is secondary compared to soil microbes in temperate and boreal vegetation zones (Berg and Laskowski 2006). However, soil fauna can have an important role in soil formation and nutrient cycling by mixing the leaf litter into deeper soil layers and releasing nutrients by grazing both the leaf litter and litter-associated microbes (Lavelle and Spain 2001; Hättenschwiler and Gasser 2005). Soil fauna also interacts with soil and litter-associated microbes meaning that animals and microbes can stimulate each other's activity during the decomposition process (Coûteaux *et al*. 1991, 1996; Lavelle and Spain 2001; Hättenschwiler and Gasser 2005). At present, information about litter-mediated CO_2 effects on litter-feeding soil animals is scarce, inconsistent, and mainly limited to woodlice (i.e. terrestrial isopods, important detritivores in the temperate forests). For instance, leaf litter consumption by woodlice has been observed to decrease (Hättenschwiler *et al*. 1999), increase (Cotrufo *et al*. 1998b) or not to change (Hättenschwiler and Bretscher 2001), although all of these studies have reported significant leaf litter quality changes (e.g. clear decrease in N) due to elevated CO_2. In our microcosm study (Kasurinen *et al*. 2007), the leaf litter consumption rates by woodlice were poorly related to the measured chemical components, and only a marginally significant and transient decrease in consumption rates were observed when animals were fed with N-poor and phenolic-rich CO_2 litter.

The complexity of the soil food web itself can be an important factor for modifying the CO_2 effects on the subsequent decomposition (Coûteaux *et al*. 1991; Coûteaux and Bolger 2000). For instance, the decomposition rates of CO_2-enriched sweet chestnut litter exposed to simple food webs

Table 2 Summary of CO_2 effects on subsequent leaf litter decomposition (absolute mass loss). Symbols: ↔ = no change, ↓ = decrease, (↓) = slight decrease, ↑ = increase, * = CO_2 environment enhances the negative litter-mediated CO_2 effect, ** = genotype-dependent CO_2 response, (*) = CO_2 environment effect on mass loss same regardless of the litter origin. Only data from OTC- and FACE-studies with soil-growing trees and naturally abscised leaf litter was included. Abbreviation: nd = not determined.

Tree species/community	**Mass loss**		**Reference**
	Decomposition environment		
	Ambient CO_2	**Elevated CO_2**	
Acer rubrum	↔	↔	Finzi *et al.* 2001
A. rubrum	↔	↔	Finzi and Schlesinger 2002
Betula papyrifera (Native placement + Common garden)	↓	↓*	Parsons *et al.* 2004
B. papyrifera (Common substrate)	↔	↔	Parsons *et al.* 2004
B. pendula (Exp. 1)	↓**	nd	Kasurinen *et al*. 2006
B. pendula (Exp. 2)	↓**	nd	Kasurinen *et al*. 2006
B. pendula (Exp. 3)	↔	nd	Kasurinen *et al.* 2006
Cornus florida	↔	↔	Finzi *et al.* 2001
C. florida	↔	↔	Finzi and Schlesinger 2002
Cercis canadensis	↔	↔	Finzi *et al.* 2001
C. canadensis	↔	↔	Finzi and Schlesinger 2002
Liquidampar styraciflua	↔	↔	Finzi *et al.* 2001
L. styraciflua	↔	↔	Finzi and Schlesinger 2002
Pinus taeda	↔	↔	Finzi *et al.* 2001
P. taeda	↔	↔	Finzi and Schlesinger 2002
P. sylvestris	↔	nd	Kainulainen *et al*. 2003
Populus alba	(↓)	↔	Cotrufo *et al.* 2005
P. × euramericana	(↓)	↑	Cotrufo *et al*. 2005
P. nigra	(↓)	↑	Cotrufo *et al.* 2005
Quercus ilex	nd	↓	de Angelis *et al.* 2000
Q. myrtifolia (Exp. 1)	↔	nd	Hall *et al*. 2006
Q. myrtifolia (Exp. 2)	↔	↑(*)	Hall *et al.* 2006

(microflora+Protozoa) were lower than that of control litter, whereas exposure to more complex foodwebs (microflora + Protozoa + higher soil fauna including nematodes, springtails and woodlice) led to higher decomposition rates of the CO_2-enriched litter when compared to control litter (Coûteaux *et al*. 1991; Coûteaux and Bolger 2000). In a recent FACE study with paper birch, trembling aspen and sugar maple, elevated CO_2 increased the total tree productivity but simultaneously decreased the abundance of total soil fauna, springtails and mites after a four-year-exposure period (Loranger *et al*. 2004). At the same time, Parsons *et al*. (2004) observed a decrease in the subsequent decomposition of birch leaves in the same CO_2 plots. Both results (Loranger *et al*. 2004; Parsons *et al*. 2004) indicate that the CO_2-induced changes in litter quality of both above- and below-ground compartments can be manifested in the soil food web and in its functioning in the deciduous tree stands. In a FACE study with loblolly pine trees, Hansen *et al*. (2001) noticed a consistent trend toward lower microarthropod abundance in elevated CO_2, but in this case the driving mechanim was suggested to be some change in the microbial resource base or habitat (i.e., non-litter CO_2 effects), as this negative animal response was observed early after the onset of the CO_2 treatment and before any CO_2-induced quality changes in leaf litter was even possible to detect. In contrast, Haimi *et al*. (2005) found only minor CO_2-induced changes in decomposer fauna at the Scots pine stand after six years of CO_2 exposure (i.e., densities of one mite suborder and one springtail species decreased), but since they did not study litter quality it is not possible to state whether there was also a lack of litter response to elevated CO_2.

The few available studies indicate that CO_2-induced decreases in litter N concentrations may be maintained at the initial stages of decomposition (Coûteaux *et al*. 1991, 1996; Parsons *et al*. 2004; Cotrufo *et al*. 2005). Although the lower N concentrations at the early stages of decomposition may decrease decomposition rates, the effect of N concentration is reversed during the later stages of decomposition (Berg and Laskowski 2006). Thus, the CO_2-induced changes in N concentrations of leaf litter could in fact lead to more complete decomposition (i.e., humus formation decreases), although it must be kept in mind that N is not the only nutrient controlling the litter disappearance rates at the later stages of decomposition (Berg and Laskowski 2006). For instance, Coûteaux *et al*. (1991) showed in their microcosm study that the early stage of decomposition of CO_2-enriched sweet chestnut litter was always lower than that of more N-rich control litter, but during the later stages the decomposition rate of N-poor and CO_2-exposed litter in fact enhanced. In another incubation study with sweet chestnut litter (Coûteaux *et al*. 1996), lignin decay started earlier in N-poor CO_2 litter than in more N-rich control litter, whereas Parsons *et al*. (2004) did not observe any significant change in lignin decomposition rates of birch litter both produced and incubated under elevated CO_2. Although a laboratory study (King *et al*. 2001b) indicated that initial CO_2 treatment effects on condensed tannins (i.e. CO_2-induced increase) in sugar maple leaf litter may quickly disappear, a longer field incubation experiment in high CO_2 environment (Parsons *et al*. 2004) indicated that the initial CO_2-induced increases in the concentrations of condensed tannins in paper birch leaves are not necessarily immediately neutralized by microbes or physical effects such as leaching. Elevated CO_2 has not been found to affect the subsequent disappearance rates of condensed tannins in trembling aspen leaves (King *et al*. 2001a) or total phenolics and monoterpenes in Scots pine needles (Kainulainen *et al*. 2003).

According to the concept of progressive N limitation, declining N mineralization (i.e. microbial N release from litter and SOM) is one of the indicators of incipient PNL in N-limited ecosystems (Luo *et al*. 2004). So far the results of CO_2 enrichment experiments have been ambiguous and there is no clear support for either positive (Zak *et al*. 1993) or negative feedback (Diaz *et al*. 1993) on soil N cycling as various studies have reported either increases, decreases or no change in the rate of N immobilization and mineralization under elevated CO_2 (Finzi and Schlesinger 2003; Holmes *et al*. 2003; Zak *et al*. 2003; Cotrufo *et al*. 2005; Holmes *et al*. 2006). However, the CO_2-response of microbial functioning may change over time, as Holmes *et al*. (2003) first observed no change in N transformations beneath CO_2-exposed trees, but later they measured increased gross N mineralization rates and NH_4^+ immobilization from the same experimental plots (Holmes *et al*. 2006). In the same FACE experiment with trembling aspen, paper birch and sugar maple also soil microbial activity involved with the degradation of plant cell wall components was stimulated (Larson *et al*. 2002; Phillips *et al*. 2002; Chung *et al*. 2006). Hence, N turnover by microbes was increased, but there was no proof of altered soil N cycling (Holmes *et al*. 2006). In a loblolly pine dominated forest microbial-N immobilization was not increased under elevated CO_2 and although the rate of net N mineralization declined over the first six years of experiment, this decline was not significantly more rapid under elevated CO_2 (Finzi *et al*. 2006). Previously Zak *et al*. (2000a) concluded that only in systems where the CO_2-induced increase in plant litter production clearly overcomes the pre-existing SOM pools, soil N cycling may be changed. In some ecosystems the direction and magnitude of N and C cycling response may depend more on changes in below-ground litter inputs than in above-ground litter inputs (Zak *et al*. 2000b; Matamala *et al*. 2003; de Graaff *et al*. 2006). Taken together, although some decomposition and element cycling processes in soil may be altered due to elevated CO_2, at the moment there is no consistent evidence of CO_2-induced and microbe-mediated PNL in temperate forests. Thus, more long-term studies (>7 years) including both above- and below-ground litter sources and with more complex soil food webs are needed to get an overall picture of the decomposition and element cycling processes.

EFFECTS OF ELEVATED O_3 ALONE AND IN COMBINATION WITH CO_2

Litter quantity and quality responses

Since the average effect of O_3 on tree growth is negative (Grantz *et al*. 2006), it can be assumed that in the future O_3 will decrease the leaf litter inputs to the soil, if some other environmental factor (e.g. elevated CO_2) does not counteract this negative effect. There are only a few O_3 and $CO_2 \times O_3$ interaction studies where the actual leaf litter production has been reported. In most recent studies, Liu *et al*. (2005) reported clear O_3-induced decreases in leaf litter masses in the FACE experiment with trembling aspen and paper birch trees, whereas in our OTC study no clear O_3 effects on silver birch leaf litter mass were found over a three-year-exposure period (Riikonen *et al*. 2004). In the above FACE study, the negative O_3 effect on leaf litter production was detected mainly under ambient CO_2 levels, although elevated O_3 had also a tendency to diminish the positive effect of CO_2 on leaf production in the combination treatment (Liu *et al*. 2005). O_3 stress has also been observed to accelerate foliar senescence and abscission (Findlay *et al*. 1996; Andersen 2001, 2003; Riikonen *et al*. 2004), but based on scarce data it seems that this O_3 effect is mainly observed under ambient CO_2 conditions (Riikonen *et al*. 2004).

If leaf senescence is accelerated due to O_3 stress and N resorption from leaves is not complete at the time of leaf abscission this could lead to leaf litter with increased N levels (Findlay and Jones 1990; Uddling *et al*. 2005). So far O_3 effects on N resorption or leaf litter N have been highly variable (Scherzer *et al*. 1998; Lindroth *et al*. 2001; Uddling *et al*. 2005). Previously Lindroth *et al*. (2001) have also reported that the elevated O_3 responses were modified by the tree species and prevailing CO_2 levels. First of all, O_3 stress decreased both the N resorption efficiency and C:N-ratios in paper birch leaves, but not in trembling aspen, and secondly, under the combination treatment, the negative O_3

Table 3 Summary of O_3 effects on leaf litter chemistry. Treatment effect % = (the O_3 treatment average response minus the control treatment average response divided by the control treatment average response) × 100. Negative values indicate decrease and positive values increase in chemical concentration or C:N-ratios, and 0 denotes for no change. Symbols: * = a significant O_3 effect ($P \leq 0.1$) and ** = tree community-dependent O_3 response. Only data from OTC- and FACE-studies with soil-growing trees and naturally abscised leaf litter was included. Abbreviation: nd = not determined.

Tree species/community	N	P	C:N-ratio	Lignin	Condensed tannins	Reference
Betula papyrifera	0	nd	+3	-12	+4	Parsons *et al*. 2004
B. pendula	-6	-15*	+8	+1	+5	Kasurinen *et al.* 2006, 2007[1]
B. papyrifera-Populus tremuloides	-18*	-27*	+23**	-5	+94*	Liu *et al.* 2005, 2007
Pinus sylvestris	-2	-3	nd	nd	nd	Kainulainen *et al.* 2003
Populus tremuloides	-7*	-19*	+7**	+26	+79*	Liu *et al*. 2005, 2007
Average response (n =4-5)	**-7**	**-16**	**+10**	**+3**	**+46**	

[1] data averaged over three experiment years

effect on N resorption efficiency in birch leaves was cancelled due to elevated CO_2, whereas the C:N-ratios of birch leaves were increased even more than in the single CO_2 treatment (Lindroth *et al*. 2001). In our small O_3 data compilation with soil-growing trees and naturally abscised litter (**Table 3**), only one study (Liu *et al.* 2005) reported marginally significant O_3 effects on aspen and aspen-birch litter N concentrations (decrease) and C:N-ratios (increase) while other studies showed no clear O_3 response patterns in litter N and C:N-ratios. In addition, Kasurinen *et al*. (2006) or Parsons *et al*. (2004) did not either observe any significant $CO_2 \times O_3$ effects on leaf N concentrations or C:N-ratios in two different birch species. In fact, in both studies the negative CO_2 effect on leaf litter N concentrations and C:N-ratios were seen regardless of prevailing O_3 levels, as elevated CO_2 decreased N concentrations and increased C:N-ratios in the CO_2+O_3 treatment also (Parsons *et al*. 2004; Kasurinen *et al*. 2006). Although in the study of Liu *et al.* (2005) both elevated CO_2 alone and O_3 alone decreased litter N concentrations, the combination treatment did not show additive response (e.g. either CO_2 or O_3 did not exacerbate each other's influence).

Table 3 shows that all the significant O_3-induced decreases in litter P concentrations have been observed in birch or aspen experiments. In both studies the O_3-induced decrease in P concentrations was observed mainly under ambient CO_2 (Kasurinen *et al*. 2006; Liu *et al*. 2007). In addition, Kasurinen *et al*. (2006) observed that in silver birch O_3 reduced the concentrations of Mn, Zn and B in both green foliage and leaf litter, and that these O_3-induced decreases in nutrients were detected also under elevated CO_2 (Kasurinen *et al*. 2006). Since the leaf litter mass was not significantly altered by O_3 treatments (Riikonen *et al*. 2004), fluxes of some of these nutrients to the soil (e.g. B and Mn) were somewhat decreased (Kasurinen *et al*., personal data). Liu *et al*. (2007) reported O_3-induced decreases in aspen and aspen-birch litter S, Ca and Zn concentrations. In contrast to our study (Kasurinen *et al.* 2006), the negative O_3 effect on Zn was seen only under ambient CO_2 (Liu *et al.* 2007). Because of decreased litter production, elevated O_3 decreased statistically significantly the fluxes of N, P, S, K, Ca, Mg, Cu, Cu and Zn, and marginally statistically significantly the flux of Mn to the soil (Liu *et al.* 2007). Based on this limited data, it seems that O_3 is capable of inducing some changes in leaf litter nutrient composition, but these responses are less consistent than those induced by elevated CO_2, and under combined exposure situation elevated CO_2 may either dominate over (Parsons *et al*. 2004; Kasurinen *et al*. 2006) or totally cancel the O_3 responses (Lindroth *et al*. 2001; Liu *et al.* 2007).

Ozone is a phytotoxic gas, and under O_3 stress trees may reduce their C assimilation and photosynthate production. On the other hand, O_3 is known to activate phenylpropanoid metabolism regardless of the potentially decreased photosynthesis (Kangasjärvi *et al*. 1994; Koricheva *et al*. 1998; Dizengremel 2001; Podila *et al*. 2001). Although some greenhouse studies have shown O_3-induced increases in leaf litter total phenolics (Findlay *et al*. 1996), long-term field experiments have not usually revealed any clear O_3-induced changes in phenolics (Kainulainen *et al*. 2003; Kasurinen *et al*. 2007; but see Liu *et al*. 2005). The discrepancy between the greenhouse and field studies is probably partly due to the differences in the O_3 exposures used. For instance, Findlay and Jones (1990) used high levels of O_3 for a short exposure period (i.e. O_3 level of 200 ppb for 5 hours), whereas in recent field studies O_3 exposure levels have been usually only about two times the ambient levels (e.g., approximately 60 ppb) and exposure has continued for several consecutive growing seasons (Kainulainen *et al*. 2003; Kasurinen *et al*. 2007). However, in our OTC study with birch some O_3 effects on individual phenolic compound groups manifested gradually towards the end of the experiment (Kasurinen *et al*. 2007), this result thus emphasizing a need for long-term (3 years or more) studies in order to properly assess chronic O_3 stress effects on tree leaf litter quality. Liu *et al*. (2005) reported increased condensed tannin concentrations under O_3 exposure (**Table 3**) and interestingly, this stimulating effect of O_3 was most apparent in the combined CO_2+O_3 treatment. However, other studies show that O_3 does not significantly affect the condensed tannins (Lindroth *et al*. 2001; **Table 3**), and under the combination treatment the CO_2 effect seems to dominate over the O_3 effect (Parsons *et al*. 2004; Kasurinen *et al*. 2007). Of other C-based compounds, high O_3 levels (100 ppb) seem to induce stress lignin production in foliage (Cabané *et al*. 2004), but when O_3 stress is milder, the O_3 response of lignin (**Table 3**) and other cell wall components has ranged from no change to slight decrease or increase, the first response pattern being the most commonly observed one (Boerner and Rebbeck 1995; Kim *et al*. 1998; **Table 3**). As with total phenolics, under the combination treatment the O_3 effect is usually dominated over by the CO_2 effect and therefore the combination treatment effects on cell wall chemistry are largely similar as the effect of elevated CO_2 alone (Parsons *et al*. 2004; Kasurinen *et al*. 2006). Limited data also indicates that monoterpene concentrations do not change due to O_3 stress either under ambient or elevated CO_2 levels (Kainulainen *et al*. 2003).

Decomposition and soil food web responses

A few studies indicate significant O_3-induced decreases in the subsequent decomposition rates in ambient O_3 environment (Findlay and Jones 1990; Findlay *et al*. 1996), but other studies report no change (Boerner and Rebbeck 1995; Scherzer *et al*. 1998; **Table 4**) or genotype-dependent slow down in the decomposition rates, but only after several exposure seasons (**Table 4**). Interestingly, Parsons *et al*. (2004) did not observe any changes in the absolute mass loss of O_3 exposed leaf litter when paper birch litter was incubated in its original plot (elevated O_3 plot) or common garden (ambient air) or when leaf litter from control trees were incubated in high O_3 plots (**Table 4**). However, when leaf litter from control trees was incubated in high O_3+ambient CO_2 plots, the relative mass loss rates (k-values) were significantly accelerated leading to shortened maximum residence times (time-to-95%-loss) (Parsons *et al*. 2004). The effects of combination treatment on the absolute mass

Table 4 Summary of O_3 effects on subsequent leaf litter decomposition (absolute mass loss). Symbols: ↔ = no change, ↓ = decrease, ** = genotype-dependent O_3 response. Only data from OTC- and FACE-studies with soil-growing trees and naturally abscised leaf litter was included. Abbreviation nd = not determined.

Tree species/community	Mass loss		Reference
	Decomposition environment		
	Ambient O_3	Elevated O_3	
Betula papyrifera (Native placement + Common garden)	↔	↔	Parsons *et al.* 2004
B. papyrifera (Common substrate)	↔	↔	Parsons *et al.* 2004
B. pendula (Exp. 1)	↔	nd	Kasurinen *et al*. 2006
B. pendula (Exp. 2)	↔	nd	Kasurinen *et al*. 2006
B. pendula (Exp. 3)	↓**	nd	Kasurinen *et al.* 2006
Pinus sylvestris	↔	nd	Kainulainen *et al*. 2003

loss were similar to that of CO_2 alone meaning that elevated O_3 did not modify the negative CO_2 effects on leaf litter decomposition in the original or common garden placement, and that the stimulating effect of elevated O_3 environment itself on k-values of common substrate was not manifested under elevated CO_2 (Parsons *et al*. 2004). On the other hand, Kim *et al*. (1998) observed that elevated O_3 concentrations both during the litter production (quality effects) and decomposition (environment effects) slowed down the mass loss rates of broomsedge-blackberry litter mixture. The authors (Kim *et al*. 1998) suggested that the reduced decomposition rates of litter collected from O_3 exposure were related to increased lignin concentrations in blackberry leaves, whereas the possible explanations for the retarded overall decomposition in high O_3 environment could be decreased microbial activity (Larson *et al*. 2002; Phillips *et al*. 2002) or altered fungal community composition (Chung *et al*. 2006) in soil. Furthermore, FACE studies show that under the combination exposure elevated O_3 can suppress the CO_2-induced enhancement of soil microbial activity and thereby C compound decomposition (Larson *et al*. 2002; Phillips *et al*. 2002).

Soil fauna responses to elevated O_3 are less studied and more variable. Kasurinen *et al*. (2007) observed that leaf litter exposed to elevated O_3 alone and in combination with CO_2 did not consistently alter woodlice leaf litter consumption rates in a laboratory study. In contrast, Loranger *et al*. (2004) have demonstrated that elevated O_3 exposure as an individual treatment can decrease the abundance of microbial-feeding mites (Acari) in the experimental plots, but that under combination treatment both O_3 and CO_2 effects are negated and result is no net change in the total soil fauna abundance.

Boerner and Rebbeck (1995) reported that in their OTC experiment more N was mineralized from leaf litter of yellow-poplar produced under ambient and doubled O_3 air than from that produced under O_3-filtered air, but there was no significant difference between the ambient and doubled O_3 treatments. In a study with single and combination treatments, Parsons *et al*. (2004) did not find any clear O_3 effect on N dynamics in decomposing leaf litter while in the combination treatment elevated CO_2 effect dominated over the O_3 effect so that N dynamics were similar to that in single exposure of CO_2. Kainulainen *et al*. (2003) and Parsons *et al*. (2004) did not either find any significant O_3 or CO_2+O_3 treatment effects on the C-based secondary compounds during their field litter incubations. On the other hand, in a FACE study with three temperate deciduous species (trembling aspen, paper birch and sugar maple), elevated O_3 has been observed to decrease gross N mineralization rates (Holmes *et al*. 2003), especially in combination with elevated CO_2 (Holmes *et al*. 2006). Although the above result is not universally applicable, it suggests that O_3 may have a negative feedback on N cycling in some temperate forest ecosystems and this feedback may be enhanced by the simultaneous increase in atmospheric CO_2.

CONCLUSIONS

Elevated CO_2 increases leaf litter quantity entering the soil, and at the moment FACE studies indicate that this CO_2 stimulation of litter production may be maintained over several years through increased N uptake or NUE. However, if N redistribution in soils occurs (i.e. plant available N decreases), positive effects of elevated CO_2 on forest NPP and litter production may be declined over time. Elevated O_3 alone can decrease leaf litter quantity and increase leaf abscission rates, but due to a paucity of data an average trend in the combined exposure cannot be stated yet. However, a majority of the current CO_2 and O_3 litter studies have been conducted with young trees. Since tree responsiveness (e.g. growth responses) to CO_2 and O_3 may be partially dependent on tree developmental stage or age, more litter and NPP studies with mature trees or non-expanding forests are still needed.

Both elevated CO_2 and O_3 have the potential to alter leaf litter quality, especially in deciduous trees. However, the effects of CO_2 and O_3 on litter chemistry are inherently more difficult to detect than those on green foliage mainly because both gases can also affect leaf senescence processes and thereby increase variability. Elevated CO_2 can especially change the C:N-ratio as both the N and phenolic compound concentrations are usually altered (concentrations of N decreases and e.g. that of condensed tannins increases), whereas N resorption efficiency is not affected by the CO_2 enrichment. Based on recent studies, elevated O_3 effects are mainly seen in litter nutrient concentrations (e.g. P concentrations and some micronutrient concentrations may decrease), whereas O_3 stress effects on leaf litter non-structural and structural C compounds are less apparent or became only apparent, when O_3 concentration is higher than 100 ppb. Under the combined exposure, the CO_2 effect usually dominates over the O_3 effect, and leaf litter quality is usually similar although not necessarily identical to that observed in elevated CO_2 alone.

A majority of the field incubation studies have not found any significant CO_2- or O_3-induced reductions in the subsequent decomposition rates (i.e. mass loss, C and N dynamics). The lack of responses in litter decomposition studies is probably partly due to the low sensitivity of the techniques used such as litter bag studies. However, there are some exceptions, as recent longer-term exposure studies with soil-growing deciduous trees have revealed that both elevated CO_2 and O_3 effects on the subsequent decomposition rates can be negative or that high CO_2 or O_3 environment itself can also modify decomposition rates. Some CO_2 effects on initial leaf litter quality (e.g. decreased N concentrations, increased condensed tannin concentrations) may persist throughout the decomposition, whereas elevated O_3 effects on N and C dynamics in the decomposing leaf litter have been negligible. Under combined exposure no general decomposition response pattern has yet emerged although some studies indicate that under the combination treatment the N dynamics seems to be similar as that in elevated CO_2 alone.

Interestingly, recent FACE experiments also show that especially the functioning of primary decomposers (mic-

robes) may be affected by the increasing CO_2 and O_3 levels. The few available studies show that elevated CO_2 can stimulate microbial activity, whereas O_3 dampens it, and under combined exposure, O_3 can suppress the CO_2-induced enhancement of soil microbial activity. However, recent FACE studies do not show consistent evidence of microbe-mediated progressive nitrogen limitation in temperate forests due to CO_2 increment. There is also a paucity of data regarding the O_3 effects alone and in combination with CO_2 on soil N cycling especially in boreal forests.

Taken together, the experiments represented here show that there are some combined effects that cannot be predicted on the basis of single exposures and therefore, in order to study realistically climate change effects on decomposition and nutrient cycling processes in the forests, effects of increasing CO_2 and O_3 must be studied in combination. In addition, in the future the ongoing global climatic warming may modify the CO_2 and O_3 responses in forests. For instance, temperature rise can increase soil drought and thereby either enhance or control over the effects of CO_2 and O_3 on decomposition and nutrient cycling processes.

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