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Long-term effects of ozone on CO_2 exchange in peatland microcosms

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ABSTRACT

Effects of elevated tropospheric ozone concentration on the CO_2 exchange of peatland microcosms and the photosynthetic capacity of the dominating sedge, *Eriophorum vaginatum*, were studied in a four-year open-field experiment. The net ecosystem CO_2 exchange and the dark respiration rate of the microcosms were measured with the closed chamber method. The CO_2 assimilation rate and chlorophyll fluorescence (maximal photochemical efficiency of PSII, F_v/F_m) of *E. vaginatum* leaves were also measured. The gross photosynthesis rate of the microcosms was transiently decreased by ozone exposure during the first year. During the fourth year, the gross photosynthesis and dark respiration rate were both slightly increased by ozone exposure but this was due to the increased density of sedge leaves and no difference was found in F_v/F_m. In overall, chronic ozone exposure had only slight effect on the CO_2 exchange of the peatland microcosms.

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1. Introduction

The global background ozone concentration has approximately doubled (daily mean from 20 ppb to 40 ppb) over the industrialized period (Vingarzan, 2004). Although the highest peak ozone concentrations in northern Europe are estimated to turn to slow descent during this century due to the emission reductions of ozone precursors, the background concentration is likely to continue its increase during the 21st century (Vingarzan, 2004; Laurila et al., 2004a,b, Ashmore, 2005). Tropospheric ozone is a major greenhouse gas with estimated radiative forcing of 0.35 W m^{-2} (Foster et al., 2007), but it also has negative effect on CO_2 assimilation rate and growth of several plant species (Andersen, 2003). The resulting decrease in the land-carbon sink could contribute even more to global warming than the direct radiative forcing due to tropospheric ozone increases by 2100 (Sitch et al., 2007).

Effects of tropospheric ozone on crop plants and trees with commercial importance have been widely studied during the last decades (reviewed by Morgan et al., 2003; Felzer et al., 2007; Wittig et al., 2007, 2009). For example, Wittig et al. (2007) estimated in their meta-analysis of 61 articles that the 20 ppb increase in ozone concentration during the last century has decreased the light-saturated photosynthesis rate of trees on average by 11%. In natural herbaceous plant species, wide variety of different ozone responses has been reported. Negative effect on photosynthesis processes has been reported on both vascular plants (*Trifolium repens* and *Lolium perenne* in Hayes et al., 2009) and bryophytes (*Polytrichum commune* and *Spaghnum recurvum* in Potter et al., 1996). Shoot growth is often assumed to decrease under ozone exposure but responses are variable and even growth stimulation has been reported in some species (Pleijel and Danielson, 1997; Franzaring et al., 2000; Timonen et al., 2004).

The effects of ozone on below-ground processes are at least as variable as, and not necessary consistent with, the effects on photosynthesis or biomass production. In general, impaired photosynthesis decreases the root growth and allocation of photosynthesis products to the roots (Andersen, 2003). Also, the translocation of photosynthate can be directly inhibited by ozone (Landolt et al., 1997; Grantz and Yang, 2000). This can lead to the decreased soil respiration through the decreased root respiration and root exudation (Edwards, 1991; Pregitzer et al., 2006). However, the connection between the CO_2 assimilation in leaves and soil respiration is not always straightforward. In a three year experiment with silver birch (*Betula pendula*), ozone exposure had cumulative stimulating effect on the soil respiration (Kasurinen et al., 2004) but no significant effect on the CO_2 assimilation of the leaves (Riikonen et al., 2005). In cotton (*Gossypium barbadense*) and melon (*Cucumis melo*), ozone decreased the CO_2 assimilation rate but increased the

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root respiration rate (Grantz et al., 2003) and Matyssek et al. (2010) reported similar effects in beech (*Fagus sylvatica*). In overall, the effects of ozone stress on photosynthesis and carbon allocation are highly species specific and dependent on the prevailing environmental conditions and experimental design (Potter et al., 1996; Franzaring et al., 2000; Nussbaum et al., 2000; Andersen, 2003; Grantz et al., 2006), which makes the prediction of the effects on the carbon balances of different ecosystems susceptible to errors.

Northern mires are important storages of carbon varying from sink to a source for atmospheric CO_2 (Alm et al., 1997; Turunen et al., 2002). Excluding abiotic processes, such as leaching and fires, the CO_2 balance of the ecosystem is mainly regulated by photosynthesis of the mire plants and microbial respiration in the peat. In general, increasing tropospheric ozone concentration is believed to decrease the photosynthetic capacity and biomass production of plants and to indirectly affect the soil processes (Andersen, 2003). In addition, ozone stress increases the dark respiration rate of plants, consequently decreasing the net CO_2 uptake (Landolt et al., 1997; Biswas et al., 2008). In growth chamber studies with peatland microcosms, the exposure to 50–200 ppb ozone concentration caused moderate changes in the ecosystem CO_2 exchange (Niemi et al., 2002; Rinnan et al., 2003). The 6–7 week O_3 exposure temporarily increased the rate of ecosystem dark respiration but did not affect the gross photosynthesis.

The short-term studies with peatland microcosms (Niemi et al., 2002; Rinnan et al., 2003) express the need of long-term ozone exposure studies in more natural conditions. In this study, we assessed the long-term effects of moderately elevated O_3 concentration on the CO_2 exchange of peatland ecosystem. The peatland microcosms were exposed to elevated O_3 concentration that was 1.6–1.8 fold compared to the continuously monitored ambient level. The exposure was continued for four growing seasons and conducted in open-field conditions in order to assess the possible effects of increasing background ozone concentrations on natural ecosystems. We also measured the CO_2 assimilation and chlorophyll fluorescence of leaves of *Eriophorum vaginatum* L., the dominant vascular plant on the studied peatland ecosystem. Carbon dioxide production potential of peat was measured in laboratory after three years of exposure. The effects of ozone on methane dynamics, microbial community composition and root exudation in the same microcosms are discussed in Mörsky et al. (2008).

2. Material and methods

2.1. Ozone exposure

Peatland microcosms were exposed to elevated ozone concentration for four growing seasons (targeted 2× ambient). The study was conducted in an open-air exposure field at the University of Eastern Finland Research Garden in Central Finland (62°13′N, 27°35′E, 80 m a.s.l.). In total, 96 microcosms (10.5 cm in diameter, 40 cm in depth) with intact vegetation and peat layers were cored from a low-sedge *Sphagnum papillosum* pine fen, Salmisuo, in Ilomantsi (62°47′N, 30°56′E, 145 m a.s.l.) at the end of May 2003 (for detailed site description, see Saarnio et al., 1997). The PVC tubes were sealed at the bottom immediately after coring of the microcosms and transported to the exposure field consisting of four control, and four ozone exposure plots. The microcosms were randomly divided into eight groups, 12 microcosms for each plot. In the beginning of the experiment (in 26 June 2003), the microcosms were embedded into the soil to keep the peat temperature as natural as possible. Peat temperature was monitored in each plot at the depth of 20 cm with 1 h intervals. Water table in the microcosms was maintained at the top of the PVC tubes by watering them with distilled water when needed. The number of living sedge leaves in each microcosm was counted once a month from June to August in 2003–2005 and twice per month during growing season 2006.

The vegetation cover on the microcosms consisted mainly of *S. papillosum* Lindb. with some *Sphagnum balticum* (Russow) C. Jens. and *Sphagnum magellanicum* Brid. *E. vaginatum* was the most common vascular plant and *Carex pauciflora* Lightf., *Carex limosa* L., *Andromeda polifolia* L., *Vaccinium oxycoccus* L. and *Drosera rotundifolia* L. were found in some of the microcosms.

In the first experimental year (2003), the ozone exposure lasted from 26 June to 6 October, whereas in 2004 and 2005 the treatment was running from late May to the beginning of October. The ozone was produced from pure oxygen with an ozone generator (Pacific G22, Pacific Ozone Technology Inc., Benicia, CA, USA) and the generated ozone was released to the plots through perforated tubes from the upwind direction. The ozone concentration on each plot was measured at 15 cm above the microcosms. The experimental design is described in more detail in Mörsky et al. (2008).

2.2. CO_2 assimilation and chlorophyll fluorescence

The CO_2 assimilation potential of *E. vaginatum* was measured on mid-summer in the second and third study year with open chamber method using a portable photosynthesis system (CI-510, CID, Inc., Camas, WA, USA). Measurements were done on 12 August in 2004 and 8 July in 2005 from four microcosms on each plot in ambient CO_2 concentration. The measurements were done with flow rate of 0.5 $dm^3\,min^{-1}$ in light-saturated conditions (PAR 1200 $\mu mol\,m^{-2}\,s^{-1}$) using an external light module (CI-510LA, CID, Inc., Camas, WA, USA). Gas exchange rates were allowed to stabilize for 2 min before logging. For each measurement, five leaves were clamped in a standard transparent chamber (window 6.5 cm^2, depth 1.0 cm) and the CO_2 assimilation rate was standardized for leaf area.

The chlorophyll fluorescence measurements were conducted using a portable fluorescence monitoring system (FMS 2, Hansatech Instruments Ltd., Norfolk, UK). On each plot, 12 (2003–2005) or 9 (2006) new leaves of *E. vaginatum* were measured separately, each from different microcosm. After 20 min dark adaptation of the leaves, minimal fluorescence (F_0) was measured. Maximal fluorescence (F_m) was obtained by exposing the leaf to a saturation light pulse (9400 $\mu mol\,m^{-2}\,s^{-1}$). Maximal photochemical efficiency of PSII in a dark-adapted state (F_v/F_m) was calculated as $(F_m - F_0)/F_m$ (Genty et al., 1989). The measurements were done twice in 2003 (weeks 31 and 35), three times in 2004 (weeks 26, 27 and 31) and four times in 2005 (weeks 25, 28, 31 and 34).

2.3. CO_2 production potential

Effect of the ozone exposure on microbial respiration rate in the peat was measured in laboratory. In September 2005, after three years of exposure, 24 microcosms (three from each plot) were dug up and unpacked. Peat samples were collected from the depth of 8–12 cm for the laboratory experiments and homogenized by hand. Two sub-samples of 30 ml in volume were taken from every microcosm. The peat samples were enclosed in glass bottles (volume 600 ml) and incubated in dark at 20 °C for one day before measurements. The bottles were closed with rubber stoppers and the CO_2 concentration in the bottles was measured four times with 3 h intervals by taking two 1 ml air samples from each bottle. The gas samples were analyzed immediately with infrared gas analyzer (Uras 3G, Hartmann & Braun, Frankfurt am Main, Germany) and integrator (Hewlett Packard 3392A, Palo Alto, CA, USA) using pure nitrogen as a carrier gas. Gas mixture with 391.2 ppmv CO_2 was

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