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Legacy effects of elevated ozone on soil biota and plant growth

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ABSTRACT

Many studies have examined how human-induced atmospheric changes will influence ecosystems. The long-term consequences of human induced climate changes on terrestrial ecosystems may be determined to a large extend by how the belowground compartment will respond to these changes. In a free-air ozone enrichment experiment running for 5 years, we reciprocally transplanted soil cores from ambient and elevated ozone rings to test whether exposure to elevated ozone results in persistent changes in the soil biota when the plant and soil are no longer exposed to elevated ozone, and how these legacy effects of elevated ozone influenced plant growth as compared to current effects of elevated ozone. After one growing season, the current ozone treatment enhanced plant growth, but in soil with a historical legacy of elevated ozone the plant biomass in that soil was reduced compared to the cores originated from ambient rings. Current exposure to ozone increased the phospholipid fatty acids of actinomycetes and protozoa, however, it decreased dissolved organic carbon, bacterivorous and fungivorous nematodes. Interestingly, numbers of bacterivorous and fungivorous nematodes were enhanced when soils with a legacy of elevated ozone were placed under elevated ozone conditions. We conclude that exposure to elevated [O_3] results in a legacy effect in soil. This legacy effect most likely influenced plant growth and soil characteristics via responses of bacteria and fungi, and nematodes that feed upon these microbes. These soil legacies induced by changes in soil biotic community after long-term exposure of elevated ozone can alter the responses of ecosystems to current climatic changes.

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1. Introduction

Tropospheric ozone [O_3] is recognized as an important damaging and widespread human-induced pollutant affecting agricultural and forest ecosystems (Nikolova et al., 2010; Galant et al., 2012), and poses a great threat to crop yields (Feng et al., 2008), forest productivity (Karnosky et al., 2007) and ecosystem carbon storage (Sitch et al., 2007). In the Northern Hemisphere, tropospheric [O_3] concentrations have increased from 10 ppb to 40 ppb currently (Biswas et al., 2008), and are predicted to further increase to 70–80 ppb by the year 2100 (Vingarzan, 2004; Zeng et al., 2008). Although the influence of elevated [O_3] has been studied widely from an aboveground perspective, relatively little attention has been paid to the effects of elevated [O_3] on the belowground subsystem (Andersen, 2003; Schrader et al., 2009; Chen et al., 2009; Li et al., 2012), whereas belowground responses might be critical in determining the long-term consequences of elevated [O_3] on terrestrial ecosystems (Andersen, 2003). Moreover, effects of enhanced [O_3] on soil conditions may result in long-lasting effects that can influence plant growth by altered resource availability and other abiotic and biotic mechanisms.

Recent work has shown that effects of climate change on soil may remain present even after climate change treatments have ceased (Nie et al., 2012; Meisner et al., 2013). These effects are called legacy effects (Baer et al., 2012). For example, Meisner et al. (2013) found that changes in soil biota induced by extreme weather events persisted in the soil after abiotic conditions had been reset and that this promoted later growing exotic plants while suppressing native ones. Similarly, Nie et al. (2012) reported that long-term elevation of CO_2 and temperature led to persistent

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changes in soil microbial communities that remained present when climate change treatments were terminated.

Legacy effects have been studied for [O_3] as well, but the focus so far has been on plants. For example, Andersen et al. (1997) showed that [O_3] effects on root growth and carbohydrate concentrations of ponderosa pine seedlings remained significant in seedlings even after the [O_3] treatment was ceased. Although soil biota play an important role in determining the responses of terrestrial ecosystems to climate change (Bardgett and van der Putten, 2014), whether exposure to elevated [O_3] also results in changes in the soil biota that remain present when the plant and soil are no longer exposed to elevated [O_3], and how such legacy effects of elevated [O_3] on soil biota may affect plant growth and its response to elevated [O_3] is still unknown.

In order to study the legacy effect of elevated [O_3] on soil biotic and abiotic characteristics, and how these effects influenced plant growth as compared to direct effects of elevated [O_3], we carried out a reciprocal transplant experiment with soil cores collected from rings with ambient and elevated ozone in a free-air ozone enrichment experiment (O_3-FACE) that has been running for 5 years. In each core, we grew wheat plants and determined microbial community structure, soil nematode community and soil physicochemical characteristics, and measured plant growth. We hypothesized that (1) effects of elevated [O_3] on soil biota and plant growth depend on the history of the soil, with more obvious treatment effects observed in the cores with a history of elevated [O_3], and (2) that the legacy of elevated [O_3] will influence the current effects of [O_3].

2. Materials and methods

2.1. Experimental site and design

The experiment was setup in an O_3-FACE experiment, located in a suburb of Jiangdu city in Jiangsu province of China (32°35′ N, 119°42′ E). The soil at the study site is a Shajiang-Aquic Cambosols (Typic Endoaquepts, FAO) with a sandy–loamy texture, with 15 g kg^{-1} total C, 1.5 g kg^{-1} total N, pH 6.8, 25.1% clay (<0.001 mm) and bulk density 1.2 g cm^{-3} at 0–15 cm depth (Zhu et al., 2011). The climate conditions are temperate with an average annual temperature and precipitation of 14.9 °C and 980 mm, respectively. An O_3-Free air enrichment (FAOE) experiment was established in 2007 in a rice–wheat rotation system. Rice was transplanted in mid-June and harvested in mid-to-late October. Winter wheat was sown in early November and harvested in late May or early June of the next year. Rice/wheat straw from the previous season was incorporated in the soil in which the rice/wheat was growing. No additional organic matter was incorporated during the wheat growing seasons.

Three replicate O_3-FAOE rings, each with 14.5 m in diameter, were installed at random sites within a uniform area of 4 ha to continuously provide an elevated level of [O_3] of 60 ppb from 9:00 am to 18:00 pm (this setup is hereinafter referred to as E-O_3). A mixed gas consisting of about 5% O_3 and 95% O_2 was produced at about 50 cm above the canopy height by an O_3 generator (KCF-BT0.2, Jiangsu Koner Ozone Co. Ltd, Yangzhou, China). The O_3 concentration was released on the basis of the wind direction and wind speed to achieve the elevation of O_3 within ±15% of the set point for 90% time and was measured at the center of each plot every 20s by an O_3 analyzer (Thermo Environmental Instruments, Franklin, MA, USA). Three other rings of the same size were supplied with ambient air (about 40 ppb) (hereafter referred to as A-O_3). The rings were located at 70 m distance from each other to prevent ozone spilling from one ring to another. Each ring (plot) was split into four subplots planted with four winter wheat cultivars (*Triticum aestivum* L.): Yangfumai 2 (Y2), Yannong 19 (Y19), Yangmai 15 (Y15) and Yangmai 16 (Y16). Nitrogen was applied as urea (N = 46%) and di-ammonium phosphate at a total rate of 210 kg N ha^{-1}, and was split into a basal application at planting (60%), an application at early tillering (10%), and one at elongation stage (30%). P and K were applied as di-ammonium phosphate and potassium chloride, respectively, at a rate of 90 kg P_2O_5 ha^{-1} and 90 kg K_2O ha^{-1}, which were split-applied with 60% at planting and 40% at elongation stage, respectively (Zhu et al., 2011). The current experiment was conducted during the wheat growing season of 2013, after the treatments had been running for 5 years.

In order to determine the legacy effect of elevated [O_3] on soil biotic and abiotic characteristics and its influence on plant growth, we transplanted ambient soil cores (a) to elevated rings (E) and elevated cores (e) to ambient rings (A). Each soil core (15 cm-diameter and 15 cm-depth) was kept intact while being removed from the soil by a shovel and placed into a separate plastic tube (15 cm-diameter and 15 cm-height). In each ring, there were also soil cores from the ring itself, which were dug out, placed in a tube, and placed back in the ring of origin. In each ambient ring, for each cultivar there was a core with ambient soil from that ring (Aa), and a core with soil from an elevated ring (Ae), vice versa for the E-O_3 rings (Ea and Ee). These cores were protected from the surrounding soil by the plastic tube and embedded into the soil. We had four wheat cultivars, each being planted in soil cores filled with soil collected from areas where that cultivar was grown during the previous season. In the current season, all cultivars in tubes were placed in the subplot with that same cultivar. This resulted in 4 (wheat cultivars) × 2 (ambient core + elevated core) = 8 cores in each ring. Before planting, soil biotic and abiotic characteristics (soil moisture, soil pH, total carbon and nitrogen, microbial biomass C and N and microbial (PLFA) and nematode community) from A-O_3 and E-O_3 rings were measured as background information.

Seeds of the four wheat cultivars were obtained from Yangzhou Agricultural University. Seven seeds of a particular cultivar were sown in each core on 14th of November in 2012. At the end of February, for all cores seedlings were thinned to four per core. For one core less than four seedlings survived, additional seedlings were planted that originated from the same ring but from outside the plastic tube. Fertilizers in the cores were applied at the same rate as in the E-O_3 rings. Agricultural management in the cores was also the same. At ripening stage (8th of June in 2013), five soil samples of 2.5 cm diameter and 15 cm deep were collected from each core and combined so that a composite soil sample of each soil core was obtained. At this time the cores had been exposed to the treatment for one growing season. All above-ground biomass was harvested, and roots were rinsed. Soil samples were stored at 4 °C until further analyses.

2.2. Soil and plant analyses

The total carbon (C) and nitrogen (N) in plant biomass and soil were determined by a TruSpec CN Elemental Analyzer (Leco Corporation, USA). Dissolved organic carbon (DOC) was determined using Multi N/C 3100 analyzer (Jena Corporation, Germany). Soil inorganic N (NO_3^-–N and NH_4^+–N) was extracted with 2 M KCl, and then the filtrates were determined using a flow injection auto analyzer (FIAstar 5000 Analyzer; Foss Tecator, Hillerød, Denmark). Soil microbial biomass was determined using the fumigation–extraction method (Brookes et al., 1985; Vance et al., 1987). Both soil microbial biomass C (MBC) and N (MBN) in the filtrate were determined using a Multi C/N 3100 analyzer (Jena Corporation, Germany). Soil basal respiration was determined using static alkali absorption method. Soil pH was determined with a glass electrode in 1:2.5 soil:water solution (w/v). Wheat plants from each core were partitioned into grain and litter. Litter, grain and

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