



Elevated O₃ and wheat cultivars influence the relative contribution of plant and microbe-derived carbohydrates to soil organic matter



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ABSTRACT

Soil carbohydrates are sensitive to changes in soil C inputs because of their fast turnover rates. However, the effects of elevated O₃ on the content and composition of soil carbohydrates are rarely reported in agroecosystem. The objectives of this study were to investigate the effects of elevated O₃ on the content and composition of soil neutral sugars in the two wheat cultivars with different O₃-tolerance. Our results showed that elevated O₃ decreased the total soil neutral sugars. At the wheat ripening stage, elevated O₃ increased the contents of galactose (Gal), arabinose (Ara) and mannose (Man) in the O₃-tolerant wheat and decreased the contents of xylose (Xyl), Gal and Ara in the O₃-sensitive wheat. Significant interactive effects between elevated O₃ and wheat cultivar were found in the ratios of (Man + Gal)/(Ara + Xyl) and Man/(Ara + Xyl). These two ratios increased with elevated O₃ at the wheat ripening stage in both wheat cultivars, with higher ratios observed in the O₃-sensitive wheat relative to the O₃-tolerant wheat. Our results indicated that elevated O₃ decreased the total neutral sugars and altered the relative contribution of plant- and microbe-derived carbohydrates to soil organic matter. Microbe-derived carbohydrates were dominant contribution to the total carbohydrates in the O₃-sensitive wheat. These changes in the accumulation and origins of soil carbohydrates will influence the accumulation and decomposition of soil organic matter and ecosystem functioning in agroecosystem.

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1. Introduction

Tropospheric ozone concentration (O₃) has been rising at the rate of 0.5–2% per year due to human activity (Feng et al., 2010; Singh et al., 2013) and is predicted to increase further (Vingarzan, 2004). As the most damaging and widespread phytotoxic air pollution, tropospheric O₃ poses a great threat to crop yields (Feng et al., 2008) and ecosystem carbon storage (Sitch et al., 2007), and affects the sustainable development of agroecosystem (Chen et al., 2009; Schrader et al., 2009). Although some studies have evaluated the effects of elevated O₃ on the aboveground subsystem, relatively little attention has been paid to the direct and indirect effects on soil-crop systems, especially for the accumulation and decomposition of labile soil organic matter (SOM) (Jones et al., 2009; Chen et al., 2009, 2010).

The influences of elevated O₃ on belowground are indirectly mediated by alterations in plant processes and C allocation (Andersen, 2003). Elevated O₃ has been reported to decrease the carbon allocation to roots and reduced carbohydrates levels and storage pools in O₃-exposed plants (Andersen et al., 1997). Changes in the quantity or quality of carbon flux into the soil will influence the interactions among soil organisms (Li et al., 2012; Li et al., 2013) and then alter carbon retention and mineralization in soil ecosystem (Andersen, 2003). As the labile fraction of SOM, soil carbohydrates account for about 5–25% of total SOM (Stevenson, 1994; Zhang et al., 2007). Soil carbohydrates are highly responsive to changes in C inputs to the soil because of their fast turnover rates (Schmitt and Glaser, 2011). However, the effects of elevated O₃ on the content and composition of soil carbohydrates are rarely reported in agroecosystem.

As a kind of non-cellulosic carbohydrates, soil neutral sugars initially originate from plant materials (including large proportions of pentose sugars-arabinose and xylose), however, soil microorganisms can re-synthesize a large amounts of hexoses (galactose and mannose) and deoxysugars (rhamnose and fucose) and release

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them into the soil (Cheshire, 1979; Bock et al., 2007). Therefore, both the contents and compositions of soil neutral sugars can be used to evaluate the plant-microbe relationship on SOM dynamics (Amelung et al., 1999; Medeiros et al., 2006). Despite the significant indication of soil carbohydrates on accumulation and decomposition of SOM, the knowledge about the effects of elevated O_3 on the accumulation and origins of soil carbohydrates in SOM is still lacking (Andersen, 2003).

Wheat (*Triticum aestivum* L.) is the second largest food crop with an annual production of about 650 million metric tons which is sensitive to the elevated O_3 (Zhu et al., 2011). In the Yangtze River Delta region, elevated O_3 reduced the yield of wheat by 10% in 1999 as predicted by Feng et al. (2003). Recently, some O_3 -tolerant wheat cultivars have been reported in China, which may avoid yield reduction in a high O_3 environment (Cao et al., 2009; Zhu et al., 2011). Different physiological characters and yield components responses to elevated O_3 have been reported in O_3 -sensitive and O_3 -tolerant wheat cultivars (Cao et al., 2009; Zhu et al., 2011). These distinct responses of different wheat cultivars to elevated O_3 would lead to differences in the quality and quantity of plant litter and/or roots which may in turn influence the C inputs to SOM. The objectives of this research were to investigate the effects of elevated O_3 on the contents and compositions of soil neutral sugars in the two wheat cultivars with different O_3 -tolerance. We hypothesized that (1) the effects of elevated O_3 will negatively affect the contents of soil carbohydrates and would subsequently be reflected in the relative contribution of plant and microbial derived carbohydrates to SOM; (2) the level of the above-mentioned changes in soil neutral sugars will exhibit cultivar dependence.

2. Materials and methods

2.1. Experimental site and O_3 -FACE treatments

The experiment was conducted in a suburb of Jiangdu city in Jiangsu province of China (32°35' N, 119°42' E). The soil is a Shajiang Aquic Cambosols (Chinese Soil Taxonomy, Zhu et al., 2011) with a sandy-loamy texture, 15.0 g kg⁻¹ total C, 1.59 g kg⁻¹ total N, pH 6.8,

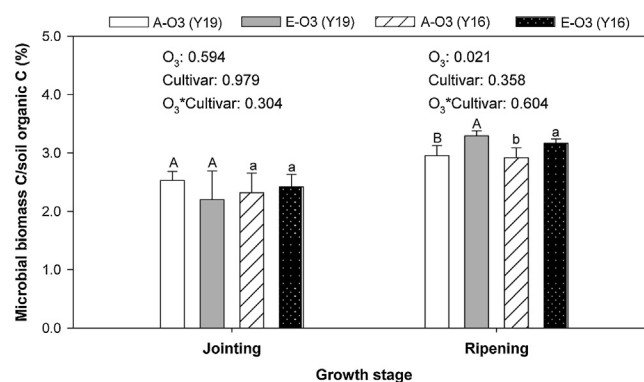


Fig. 1. The ratio of microbial biomass C to soil organic C in soil planted with O_3 -sensitive (Y19) and O_3 -tolerant (Y16) wheat under ambient (A- O_3) and elevated O_3 (E- O_3) conditions. Within each stage, capital and lowercase letters represent the significant differences between ambient and elevated O_3 for O_3 -sensitive and O_3 -tolerant wheat cultivars, respectively, bars with the same letters suggested non-significant difference in t -test ($P < 0.10$).

9.2% sand (1–0.05 mm), 65.7% silt (0.05–0.001 mm), 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 annual temperature and precipitation averages at 16 °C and 1100–1200 mm, respectively, and a frost-free period of >230 days (Zhu et al., 2011).

The experimental design was a split plot with the main plots being ambient O_3 or elevated O_3 , and sub plots being wheat cultivars (Tang et al., 2011; Zhu et al., 2011). Three replicate elevated O_3 rings, each with 14.5 m in diameter, were set randomly within a uniform area of 4 ha to continuously provide an elevated O_3 of 60 ppb over the ambient conditions (about 40 ppb), while three replicate rings, each with the same size, were set randomly within the same area for the ambient O_3 treatment. All of the rings were far enough apart to prevent O_3 from spilling over from one ring to another. Each plot under ambient and elevated O_3 conditions was split into two subplots planting with two winter wheat cultivars (*Triticum aestivum* L.) [O_3 -sensitive cultivar, Yannong 19 (Y19), and the O_3 -tolerant cultivar, Yangmai 16 (Y16)]. The experimental

Table 1
Soil and plant physicochemical variables in the soil planted with O_3 -sensitive (Y19) and O_3 -tolerant (Y16) wheat under ambient (A- O_3) and elevated O_3 (E- O_3) conditions during wheat growth season (mean \pm SD).

| | Growth Stage | A- O_3 | | E- O_3 | | Effect ^f | | |
|-----------------------------------|--------------|------------------|------------------|------------------|------------------|---------------------|--------------|----------------|
| | | Y19 | Y16 | Y19 | Y16 | O_3 | Cultivar (C) | $O_3 \times C$ |
| MBC ^a | Jointing | 401.5 \pm 25.9 | 379.5 \pm 44.9 | 319.4 \pm 58.8 | 338.5 \pm 57.4 | ns | ns | ns |
| (mg kg ⁻¹) | Ripening | 446.0 \pm 24.2 | 497.3 \pm 12.6 | 503.5 \pm 41.4 | 484.5 \pm 43.8 | ns | ns | ns |
| DOC ^b | Jointing | 421.4 \pm 56.7 | 431.3 \pm 20.0 | 459.4 \pm 50.7 | 461.1 \pm 65.9 | ns | ns | ns |
| (mg kg ⁻¹) | Ripening | 499.5 \pm 96.2 | 390.0 \pm 6.3 | 355.6 \pm 16.2 | 313.7 \pm 2.1 | 0.024 | 0.033 | ns |
| SOC ^c | Jointing | 15.90 \pm 1.11 | 16.43 \pm 0.96 | 14.67 \pm 1.42 | 13.93 \pm 1.12 | 0.065 | ns | ns |
| (g kg ⁻¹) | Ripening | 15.17 \pm 1.70 | 17.10 \pm 1.30 | 15.30 \pm 1.32 | 15.30 \pm 1.25 | ns | ns | ns |
| TN ^d | Jointing | 1.70 \pm 0.09 | 2.07 \pm 0.47 | 1.61 \pm 0.13 | 1.48 \pm 0.20 | ns | ns | ns |
| (g kg ⁻¹) | Ripening | 1.59 \pm 0.19 | 1.78 \pm 0.07 | 1.60 \pm 0.26 | 1.65 \pm 0.18 | ns | ns | ns |
| Soil C/N | Jointing | 9.34 \pm 0.43 | 8.18 \pm 1.51 | 9.11 \pm 0.25 | 9.44 \pm 0.49 | ns | ns | ns |
| | Ripening | 9.56 \pm 0.08 | 9.61 \pm 0.35 | 9.65 \pm 0.83 | 9.32 \pm 0.25 | ns | ns | ns |
| TNSC/SOC ^e | Jointing | 8.75 \pm 0.15 | 8.74 \pm 0.49 | 9.11 \pm 0.67 | 9.64 \pm 0.52 | ns | ns | ns |
| (%) | Ripening | 10.10 \pm 1.31 | 8.69 \pm 1.00 | 9.03 \pm 0.48 | 9.56 \pm 1.08 | ns | ns | ns |
| Plant C (%) | Ripening | 40.63 \pm 0.46 | 40.40 \pm 0.10 | 41.00 \pm 0.10 | 40.73 \pm 0.06 | ns | ns | ns |
| Plant N (%) | Ripening | 2.09 \pm 0.24 | 2.16 \pm 0.13 | 2.43 \pm 0.09 | 2.18 \pm 0.16 | ns | ns | ns |
| Plant C/N | Ripening | 19.59 \pm 2.04 | 18.77 \pm 1.09 | 16.86 \pm 0.65 | 18.72 \pm 1.37 | ns | ns | ns |
| Grain yield(kg ha ⁻¹) | Ripening | 6077 \pm 451 | 6160 \pm 122 | 4908 \pm 293 | 5190 \pm 370 | 0.001 | ns | ns |

^a MBC microbial biomass carbon.

^b DOC dissolved organic carbon.

^c SOC soil organic carbon.

^d TN total nitrogen in soil.

^e TNSC/SOC percentage of total neutral sugars carbon to soil organic carbon.

^f The effects were significant at $P < 0.10$; ns represents not significant.

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