



# Cascading effects of elevated ozone on wheat rhizosphere microbial communities depend on temperature and cultivar sensitivity<sup>☆</sup>

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## ABSTRACT

Tropospheric ozone (O<sub>3</sub>) concentrations have now reached levels that can potentially affect crop production in several regions of the world. The interacting effects of the elevated O<sub>3</sub> and temperature on plants are still unclear and their consequences on the rhizosphere microbial communities never studied yet. Here, we conducted a 3-week fumigation experiment on two cultivars of wheat with different tolerance to O<sub>3</sub> (Premio and Soissons) at two temperatures (20 °C and 30 °C). The impacts of O<sub>3</sub> were measured on plants physiology, rhizosphere chemical environment and microbial communities. Globally, most of the results showed that elevated O<sub>3</sub> effects were more pronounced at 20 °C than 30 °C, especially on the most O<sub>3</sub>-sensitive cultivar (Soissons). Elevated O<sub>3</sub> reduced significantly plant root biomass (up to -37% for Soissons) compared to non-fumigated plants. A decrease in the dissolved organic matter with a relative increase of aromatic compounds concentration was also observed under elevated O<sub>3</sub>, suggesting quantitative and qualitative impacts on roots exudation. While bacterial abundance was negatively affected by O<sub>3</sub> plant stress, fungal abundance was found to be stimulated (up to 12 fold compared to non-fumigated plants for Soissons at 20 °C). These changes were accompanied by modifications of the genetic structures and metabolic profiles, with a relative increase of amino acids catabolism. This fully controlled laboratory experiment showed that the effects of elevated O<sub>3</sub> on soil microbial communities i) are plant-mediated and depend on the cultivar sensitivity, ii) decrease in warming condition, iii) increase the fungi to bacteria ratio and iv) alter both the genetic structure and the metabolic activities. This study highlights the importance of considering interactive effects between pollutants and climate changes on plant-microbe relationship to better inform models and improve predictions of future states of agroecosystems.

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## 1. Introduction

Elevated concentration of ozone (O<sub>3</sub>) in the troposphere is considered as a major air pollutant of the global change. The origin of tropospheric O<sub>3</sub> consists on a double input: the first one is a downward stratosphere-troposphere exchange (Holton et al., 1995), the other one is a photochemical oxidation by UV of CO, hydrocarbons and NO<sub>x</sub> from anthropogenic origins (Chameides and Walker, 1973; Monks et al., 2015). Due to the raise of these precursors emission from vehicle and industrial sources, tropospheric O<sub>3</sub> concentration has increased by 35% since the 1950s

(Vingarzan, 2004; Cooper et al., 2014). Emission reduction policies have successfully limited the frequency and extent of O<sub>3</sub> pollution peaks (Oltmans et al., 2013). However, O<sub>3</sub> background concentrations have now reached levels that can potentially cause damaging effects on crop production in several regions of the world (Fuhrer et al., 1997; Shi et al., 2009; Mills et al., 2011; Hu et al., 2018). Indeed, O<sub>3</sub> is known to cause diverse plant oxidative stress, affecting photosynthetic process (Castagna et al., 2001; Leitao et al., 2003), damaging phospholipidic membrane (Hellgren et al., 1995), spoiling respiratory chains (Maurer et al., 1997), speeding up senescence (Pääkkönen et al., 1997), modifying enzymes involved in phenyl-propanoid metabolism (Guidi et al., 2005). A meta-analysis of experimental data on O<sub>3</sub> impact on crop yield showed that current O<sub>3</sub> levels could account for a 10% decrease in wheat grain yield (Feng et al., 2008).

The sustainable productivity of agro-ecosystems does not only

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rely on plant biomass production, but also on the activity of the rhizosphere microbial communities, which affects biogeochemical cycling, plant growth and tolerance to biotic and abiotic stresses (Philippot et al., 2013). Rhizosphere microbial communities regulate the availability of nutrients that sustain plant growth, mainly through soil organic matter mineralization (Van Der Heijden et al., 2008). The importance of the rhizosphere microbial communities for plant growth and health has been studied for decades. Rhizodeposition of carbon compounds increases microbial activity and biomass in rhizosphere soil (Hartmann et al., 2009). More than 200 different chemical compounds are released in soil by roots and are gathered under the term of rhizodeposition (Kumar et al., 2006). Through the composition of root exudates, plants shape soil microbial diversity, thereby encouraging beneficial symbioses and protective associations, ensuring supply of essential nutrients (Bakker et al., 2013). The rhizosphere's influence on microbial communities depends on the plant genotype (Bouffaud et al., 2012), plant health (Berendsen et al., 2012), growth stage (Farina et al., 2012) but although pedoclimatic factors like soil fertilization (Ai et al., 2015), elevated CO<sub>2</sub> concentrations (Drigo et al., 2010), drought (Naylor et al., 2017) or even nanoparticles exposure (Hao et al., 2018). Whilst the effects of elevated tropospheric O<sub>3</sub> on plants are well documented (Burkart et al., 2013) the literature concerning the impact of this pollutant on roots associated microbial communities is still limited and results show discrepancies. Studies on rice and wheat rhizospheres mention positive or negative effects on the abundance of microorganisms (Li et al., 2012; Ueda et al., 2016; Feng et al., 2015; Fatima et al., 2018). Results concerning microbial diversity are also contradictory. Some authors found that elevated O<sub>3</sub> increases microbial diversity (Ueda et al., 2016), others found the opposite (Chen et al., 2010) or no change (Dorhmann and Tebbe, 2005; Li et al., 2013; Wang et al., 2017). These controversial results may be due to the fact that elevated O<sub>3</sub> effects depends not only on plant species but also on cultivars (Li et al., 2013; Bao et al., 2015; Feng et al., 2015; Wang et al., 2017) and growth stage (Bao et al., 2015; Feng et al., 2015).

Another explanation of such variability in the response of rhizosphere microbial communities to elevated O<sub>3</sub> concentration could be the influence of environmental factors that often co-varies with elevated concentration of O<sub>3</sub>. For example, previous studies demonstrates interactions between the impacts of elevated CO<sub>2</sub> and O<sub>3</sub> levels (Kanerva et al., 2008; Dunbar et al., 2014; Wang et al., 2017). Although O<sub>3</sub> concentration and temperature are often reported to co-vary (Rubio and Eduardo, 2014), there is surprisingly no study on the potential effects of these two factors on below-ground microorganisms yet. Land surface temperature has increased by more than 1 °C since 1850 and will continue to rise in the 21st century under all emission scenarios (IPCC AR5 WG1, 2013). It is known that global warming has numerous effects on the physiology, development, growth and productivity of plants which may, in turn, affect rhizosphere microbial communities. For the main cereal crops, negative impacts on yield have been more common than positive ones (IPCC AR5 WG2, 2014). For wheat, which is the most widely grown crops and the fourth in production worldwide, modeling studies showed that increased growth temperatures could have accounted for a 5% decrease in grain yield over the 1980–2008 period (Lobell et al., 2011). Experimental data showed that increasing growth temperature by 1.5–2 °C over one season reduced wheat grain yield by 15–20% (Cai et al., 2016). In addition to global warming, the frequency of heat waves has increased in many regions (IPCC AR5 WG1, 2013). Heat waves can cause massive yield losses as observed for wheat after the 2003 heat wave in Europe (Ciais et al., 2005). As high irradiance promotes both O<sub>3</sub> production and elevated temperature, high O<sub>3</sub> exposure occurs generally in summer in combination with elevated

temperatures. The interacting effects of the elevated O<sub>3</sub> and warming on plants are still unclear as contradictory findings are reported in the literature (Andersen, 2003). The response of plants to a combination of stress conditions is unique and cannot be predicted from the response to the stresses applied individually (Mittler, 2002). To our knowledge, no study has ever deal with the interaction of O<sub>3</sub> and temperature on rhizosphere microbial communities.

The first objective of the present study was to disentangle the effects of elevated O<sub>3</sub> from possible other environmental factors on belowground microbial communities by carrying out a laboratory experiment in growth chambers with stringent control of environmental conditions. A 3-week O<sub>3</sub> fumigation experimentation (around 70 ppb) was conducted during the vegetative growth of two cultivars of winter wheat (Premio and Soissons) with different tolerance to O<sub>3</sub> and using a large number of replicates (n = 6). The second objective of this work was to evaluate the interactive effects of elevated O<sub>3</sub> and temperature. Here, we try to simulate conditions that can naturally occur in spring or summer with early heat wave and O<sub>3</sub> episode (Vautard et al., 2005). Thus, the experimental design described below was realized at two different temperatures (20 °C and 30 °C). The third objective was to evidence the so-called “cascading effect” by assessing the response of the whole plant-soil system to the tested factors. It is expected that the exposure to elevated O<sub>3</sub> will alter plant physiology, with consequence on roots exudates production (Andersen, 2003; Berendsen et al., 2012). Consecutively, fungal or bacterial abundance and/or structure may change with potential modification of catabolic function, what we called here “cascading effects”. To this aim, we measured the impact of elevated O<sub>3</sub> and temperature on i) plant physiological parameters, ii) rhizosphere physico-chemical characteristics and iii) microbial community structure, abundance and functions.

## 2. Material and methods

### 2.1. Soil samples, plant material and growth conditions

Samples were obtained from the ploughed layer (0–30 cm) of a cultivated Luvisol from an INRA experimental site (Les Closeaux) in Versailles, France. The soil is a silt loam (30% sand, 53% silt, 17% clay), with  $13.8 \pm 0.6 \text{ g kg}^{-1}$  total organic carbon (TOC),  $1.35 \pm 0.03 \text{ g kg}^{-1}$  total nitrogen, and a pH of 6.8. The experimental plot has been under continuous wheat since 1992. Soil samples were collected in February 2013 and sieved moist to <5 mm. Root fragments and plant debris were discarded during the sieving. Prior to use, soil samples were pre-incubated at sampling water content (pF = 3.1, corresponding to  $0.16 \text{ g water g}^{-1}$  of oven dry soil) for 3 weeks at 20 °C.

Plants of two European winter wheat (*Triticum aestivum* L.) cultivars, Premio (registered in the French crop A-list in 2007 by RAGT Semences) and Soissons (registered in the French crop A-list in 1988 by Florimond Desprez) were grown in fully controlled conditions. Seeds were kept in the dark in Petri plates on humidified absorbent paper for germination. Four germinated seeds per pot were sowed in pots filled with 1 kg of soil. After the first leaf emerged through coleoptile (BBCH stage 10), two seedlings per pot were kept. Plants were grown in two identical Adaptis A1000 growth chambers (Conviron Europe Ltd.) in the following conditions: light intensity  $200 \mu\text{mol m}^{-2} \text{ s}^{-1}$  at pot height, photoperiod 14 h, day/night relative humidity 60/70%, day/night temperature 20/20 °C or 30/30 °C.

### 2.2. Experimental design and stress treatments

Three weeks after the first leaf emerged, wheat plants at the

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