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Ozone exposure- and flux-based response relationships with photosynthesis of winter wheat under fully open air condition

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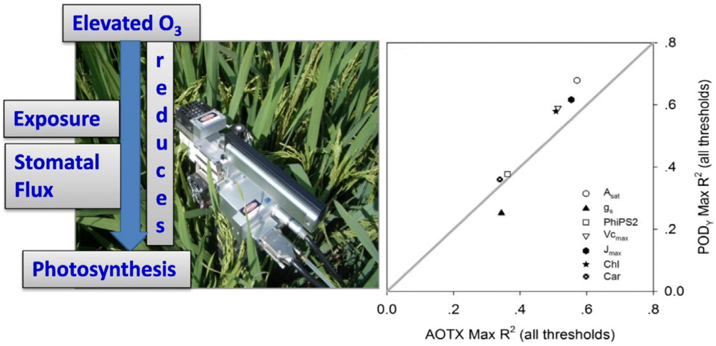
HIGHLIGHTS

- 5 modern cultivars of wheat were investigated under fully open-air field conditions.
- Regressions of photosynthetic responses with different O_3 metrics were calculated.
- Performance was slightly better for flux-based than for exposure-based O_3 metrics.
- The more robust indicators were A_{sat}, J_{max}, Vc_{max} and chlorophyll content.

GRAPHICAL ABSTRACT



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ABSTRACT

Five winter wheat cultivars were exposed to ambient (A-O_3) and elevated (E-O_3, 1.5 ambient) O_3 in a fully open-air fumigation system in China. Ozone exposure- and flux based response relationships were established for seven physiological variables related to photosynthesis. The performance of the fitting of the regressions in terms of R^2 increased when second order regressions instead of first order ones were used, suggesting that effects of O_3 were more pronounced towards the last developmental stages of the wheat. The more robust indicators were those related with CO_2 assimilation, Rubisco activity and RuBP regeneration capacity (A_{sat}, J_{max} and Vc_{max}), and chlorophyll content (*Chl*). Flux-based metrics (POD_y, Phytotoxic O_3 Dose over a threshold y nmol O_3 m^{-2} s^{-1}) predicted slightly better the responses to O_3 than exposure metrics (AOTX, Accumulated O_3 exposure over an hourly Threshold of X ppb) for most of the variables. The best performance was observed for metrics POD_1 (A_{sat}, J_{max} and Vc_{max}) and POD_3 (*Chl*). For this crop, the proposed response functions could be used for O_3 risk assessment based on physiological effects and also to include the influence of O_3 on yield or other variables in models with a photosynthetic component.

Abbreviations: AOTX, Accumulated O_3 exposure over an hourly Threshold of X ppb; A_{sat}, light-saturated net photosynthetic rate; Car, carotenoid content; *Chl*, total chlorophyll content; g_s, stomatal conductance; J_{max}, maximum rate of electron transport; PhiPS2, quantum yield of non-cyclic electron transport; POD_y, Phytotoxic O_3 Dose over a threshold of y nmol O_3 m^{-2} PLA s^{-1}; Vc_{max}, maximum carboxylation efficiency.

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1. Introduction

Tropospheric ozone (O_3) is a pollutant affecting human heath, ecosystems and food security (The Royal Society, 2008). Rural O_3 concentrations have been increasing from a background of ca. 10–15 ppb to approximately 40–50 ppb (8-h summer seasonal average) in industrialized and fast developing countries since the end of the 19th century, due to increased emissions of O_3 precursors from anthropogenic sources (The Royal Society, 2008; Cooper et al., 2014). In Asia, the fast economic development of the last decades has caused a rise at a higher pace than in other countries in parallel with higher increases in O_3 precursors, mainly NO_2 (Feng et al., 2015).

Ozone causes reductions in the yield of many sensitive crop species (Feng and Kobayashi, 2009). Wheat is one of the most important crops worldwide with an annual production of 729 million metric tons in 2014 (FAO, 2016), and its production must increase in the future in order to meet expected demands imposed by population growth (Singh et al., 2007). Model estimates suggest that global yield losses for wheat due to current ambient O_3 concentrations are 12%, with large regional differences (The Royal Society, 2008). A meta-analysis based on chamber studies found that elevated O_3 concentration (average 73 ppb, representative of future concentrations) reduced leaf photosynthesis and grain yield of wheat by 20% and 29%, respectively, as compared with plants grown in carbon-filtered air (Feng et al., 2008). It is known that the impact of O_3 increased with developmental stages, and grain filling period is the most sensitive stage; decreased photosynthesis appears to be the key driver for the yield loss (Pleijel et al., 1998). In Feng et al. (2008) meta-analysis, no significant response differences to O_3 were observed between spring wheat and winter wheat, although it is well known that there are significant differences in sensitivity to O_3 among cultivars (Feng et al., 2016).

Given the economic importance of yield, many studies have focused on crop yield responses against different exposure and dose metrics (e.g., LRTAP, 2015; Feng et al., 2012). However, studies on physiological or biochemical responses are still scarce despite the fact that these variables could represent relevant indicators of early responses to O_3 (Bagard et al., 2015; Shang et al., 2017; Sun et al., 2014) and that this type of responses are of interest to understand mechanisms of damage and for the application in modelling of O_3 effects. Exposure- and flux-response analyses of these variables provide information on which ones are more sensitive to O_3, allowing quantification of the magnitude of change for a range of O_3 exposures or accumulated O_3 uptake. It is also possible to determine which type of response functions describes better the impact of O_3 for each variable, and which are the variables showing more robust responses. Finally, knowledge of the type of exposure- and flux-responses of photosynthetic variables against O_3 is of critical importance to accurately incorporate the impact of O_3 in models with a photosynthetic component (Fares et al., 2013; Wu et al., 2016).

In last decade, O_3 risk assessment has evolved from the use of exposure-based metrics such as the AOTX (Accumulated O_3 exposure over an hourly Threshold of X ppb) to the use of flux-based metrics such as the POD_y (Phytotoxic O_3 Dose over a threshold of y nmol O_3 m^{-2} s^{-1}) (LRTAP, 2015). As the latter approach takes into account the influences of meteorological, soil moisture and phenological factors on the O_3 uptake by the plants, the use of this metric has been reported to represent an advantage over AOTX (Danielsson et al., 2003; Pleijel et al., 2004). For winter wheat, response functions for O_3-induced yield losses in subtropical regions have been proposed using AOT40 and POD_{12} (i.e., thresholds 40 ppb and 12 nmol O_3 m^{-2} s^{-1}, respectively) as the predictive O_3 metrics in the regressions (Feng et al., 2012). The main objective of this paper is to improve the assessment of O_3 impacts on wheat with respect to O_3 exposure- and flux-based metrics in a range of important physiological leaf traits. For this objective, five modern cultivars of winter wheat fumigated under fully open-air field conditions have been investigated. Cultivar-specific responses have not been taken into account as they have been previously studied in Feng et al. (2016). Further objectives are: 1) To provide O_3 exposure and stomatal flux-response relationships for photosynthesis-related variables for wheat. 2) To compare the performance of exposure- and stomatal flux-response metrics for these variables in wheat. 3) To assess which thresholds are the most suitable for establishing response relationships for both O_3 metrics. The main hypotheses to be tested are: 1) The magnitude of the physiological responses will increase at more advanced wheat developmental stages; 2) The performance of flux-based metrics for winter wheat is better than that of exposure-based metrics.

2. Material and methods

2.1. Experiment site and plant material

The experiment was carried out in a fully open-air O_3 fumigation system (O_3-FACE) in Xiaoji Town, Jiangsu Province, China (119° 42′ E, 32° 35′ N). The area has a subtropical marine climatic type with mean annual precipitation of 1100–1200 mm and mean annual temperature of 16 °C. The experimental field was placed on Shajiang Aquic Cambisols with a sandy-loamy texture, and the site has been traditionally subjected to a continuous rice/wheat or rice/rapeseed rotation. Further details on the site and climatic conditions are provided in Feng et al. (2016).

During 2007/2008 growing season, five modern wheat cultivars were used: Yannong 19 (Y19), Yangmai 16 (Y16), Yangmai 15 (Y15), Yangfumai 2 (Y2), and Jiaxing 002 (J2). Cultivation practices followed the standard local procedures (Zhu et al., 2011). Wheat seeds were sown on 13 November 2007. A total of 210 kg N ha^{-1} (60% applied at planting, 10% at early tillering and 30% at elongation stage), was applied as urea and diammonium phosphate. Furthermore, 90 kg P_2O_5 ha^{-1} and 90 kg K_2O ha^{-1} (60% at planting and 40% at elongation stage) were applied for P and K fertilization, respectively. Due to non-water-limited subtropical climatic conditions, no irrigation was required as enough rain water for growth was available.

2.2. Ozone treatments

Two O_3 treatments were applied to the wheat plants: ambient (A-O_3) and elevated (E-O_3) O_3. The latter had a targeted level of 1.5 times ambient O_3 concentrations. For each treatment, there were 3 replicated rings. O_3 fumigation started on 5 March 2008, when wheat plants were at tillering stage, and continued until the grain maturity, lasting from 9:00 h to sunset each day. For the A-O_3 treatment, the 7 h mean (9:00–16:00) averaged 52 ppb, with a maximum of 110 ppb. AOT40 varied between 8.25 and 9.45 ppm h for the E-O_3 treatment, and between 3.99 and 4.34 ppm h for the A-O_3 treatment. POD_y values (Figs. 2 and 3) were calculated on the basis of the methods and parameterizations described in Feng et al. (2012). More details on the O_3-FACE are available in Tang et al. (2011).

2.3. Gas exchange and chlorophyll *a* fluorescence measurements

Gas exchange and chlorophyll *a* fluorescence measurements were carried out at four developmental stages: heading, flowering, early- and mid- grain fillings. In each ring, a total of three fully expanded flag leaves of each cultivar were randomly selected and stems were cut underwater at predawn and immediately transported to laboratory in low light (PPFD <20 μmol m^{-2} s^{-1}). After light acclimation at 400 μmol m^{-2} s^{-1}, gas exchange and fluorescence measurements were carried out in two of the flag leaves with a LI-6400 photosynthesis system equipped with a 6400–40 leaf fluorometer (LICOR, Lincoln, NE, USA). The maximum carboxylation efficiency and the maximum rate of electron transport (Vc_{max} and J_{max}, respectively) were determined from A-C_i curves under PPFD of 1500 μmol m^{-2} s^{-1} according to Farquhar and Sharkey (1982) and Long and Bernacchi (2003). *A*-PPFD curves

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