Nitric oxide alleviates wheat yield reduction by protecting photosynthetic system from oxidation of ozone pollution

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Abstract

Accelerated industrialization has been increasing releases of chemical precursors of ozone. Ozone concentration has risen nowadays, and it's predicted that this trend will continue in the next few decades. The yield of many ozone-sensitive crops suffers seriously from ozone pollution, and there are abundant reports exploring the damage mechanisms of ozone to these crops, such as winter wheat. However, little is known on how to alleviate these negative impacts to increase grain production under elevated ozone. Nitric oxide, as a bioactive gaseous, mediates a variety of physiological processes and plays a central role in response to biotic and abiotic stresses. In the present study, the accumulation of endogenous nitric oxide in wheat leaves was found to increase in response to ozone. To study the functions of nitric oxide, its precursor sodium nitroprusside was sprayed to wheat leaves under ozone pollution. Wheat leaves sprayed with sodium nitroprusside accumulated less hydrogen peroxide, malondialdehyde and electrolyte leakage under ozone pollution, which can be accounted for by the higher activities of superoxide dismutase and peroxidase than in leaves treated without sodium nitroprusside. Consequently, net photosynthetic rate of wheat treated using sodium nitroprusside was much higher, and yield reduction was alleviated under ozone fumigation. These findings are important for our understanding of the potential roles of nitric oxide in responses of crops in general and wheat in particular to ozone pollution, and provide a viable method to mitigate the detrimental effects on crop production induced by ozone pollution, which is valuable for keeping food security worldwide.

1. Introduction

Ground-level ozone (O3) is recognized as one of the most deleterious rural air pollutants due to its powerful oxidization and phytotoxicity (Fiore et al., 2012; Li and Blande, 2015; Carriero et al., 2016). After entering the 21st century, O3 concentrations are increasing at a rate of approximately 0.5–2% per year over the northern mid-latitudes (Intergovernmental Panel on Climate Change, 2013). The rapid process of urbanization and industrialization is inevitably releasing more and more chemical precursors of O3, and leading to rising O3 concentrations worldwide (Sitch et al., 2007; Wang et al., 2007). In addition to being a greenhouse gas and harmful to human health, potential impacts of ozone on agriculture are larger than the direct impacts of climate change in some regions, with predicted up to 26% of global annual yield reductions for some crops by 2030 (Avnery et al., 2011b). Take wheat as an instance, published documents showed that ozone resulted in 6.4–14.9% of yield loss now, and this number would rise to 14.8–23.0% by 2020 (Feng et al., 2015).

Wheat is one of the most vital crops worldwide, and more than half of the world population relies on it as their primary principal food (Zhu et al., 2011; Saitanis et al., 2014; Li et al., 2016). It was estimated that global yield of wheat must increase constantly by 2% annually until 2020 to satisfy the requirements driven by growing human population and prosperity (Singh et al., 2007). Moreover, growing human population on earth means that the food demands will increase for more than 40 years (Godfray et al., 2010). However,
wheat production is confronting with great challenge due to its high O3-sensitivity (Biswas et al., 2008; Feng et al., 2008; Wilkinson et al., 2012). Large numbers of reports have shown that O3 pollution imposes negative effects on multiple aspects and levels of metabolism in plants (Ainsworth, 2008; Emerson et al., 2009; Li et al., 2013). At prime tene, O3 enters the cell of plants through stomata of leaves, then engenders multiple types of reactive oxygen species (ROS) in the apoplast, which can lead to cellular oxidative damage (Fiscus et al., 2005; Fuhrer, 2009). Visible injury induced by ROS will perform in leaves of O3-sensitive plants (Feng et al., 2014; Picchi et al., 2017). Finally, this leads to reduction of carbon assimilation. To cope with the damage of ROS, plants mobilize various mechanisms to detoxify ROS at the molecular, cellular and physiological level by redox homeostasis (Nakashima et al., 2009; Kong et al., 2012; Correa-Aragunde et al., 2009; Zeng et al., 2011; Corpas et al., 2009). Previous studies showed that NO could prevent adverse impact to plants provoked by abiotic stresses such as UV-B, herbicides, heavy metals, drought, salinity and heat, due to its redox balance regulation (Singh et al., 2012; Crawford et al., 2006; Corpas et al., 2009). Nitric oxide (NO), as a key bioactive signal molecule with diverse biological functions, plays pivotal role in multiple biological processes in plants, such as cell differentiation, energy synthesis, programmed cell death and signal transduction of stresses (Arasimowicz and Floryszak-Wieczorek, 2007; Sanz et al., 2015; Fancy et al., 2017). NO can be produced from two main pathways: nitrate reductase (NR) pathway and nitrate oxide synthase (NOS) pathway (Gupta et al., 2011). However, there is a controversy concerning the existence of NOS in plants. The presence of NOS activity has been identified in Arabidopsis thaliana (Guo et al., 2003; Crawford et al., 2006; Corpas et al., 2009). Previous studies showed that NO could prevent adverse impact to plants provoked by abiotic stresses such as UV-B, herbicides, heavy metals, drought, salinity and heat, due to its redox balance regulation (Singh et al., 2009; Zeng et al., 2011; Kong et al., 2012; Correa-Aragunde et al., 2015). For instance, NO can effectively enhance the tolerance of plants against UV-B through up-regulating activities of antioxidant enzymes in Arabidopsis, lettuce, maize and soybean (Shi et al., 2005; Santa-Cruz et al., 2014; Esrinu et al., 2016; Vanhaevelyn et al., 2016). However, little is known about the functions of NO on tolerant mechanism of wheat to O3 pollution. In the present study, we investigated endogenous NO production in response to O3, and further elucidated the effects of NO on winter wheat under O3 pollution by measuring antioxidant enzyme activity, hydrogen peroxide, malondialdehyde, electrolyte leakage, gas exchange and yield.

2. Materials and methods

2.1. Plant culture and treatments

The cultivar of winter wheat, Triticum aestivum L. cv Liangxing99 was used in this study. The experiment was performed at the Shandong Agricultural Ecosystem Research Station (35°27′26″N, 117°50′49″E), Pingyi County, Shandong Province, China. Major air pollutant sources have not been found in the vicinity of this experimental site, and the O3 concentration of ambient air was less than 40 ppb during the exposure.

The open-top chambers (OTCs) were built with 2.4 m in height, 2.6 m in diameter. The gas dispensing system of open-top chambers (OTCs) was conducted based on the previous method (Uprety, 1998). The injected O3 was produced by electrical discharge using ambient air by an O3 generator (CF-KG1, Shaniechinaimei Ltd., Beijing, China). During this period, O3 concentration of 10 cm above the wheat canopy was monitored by ozone monitor (Model 106-L, 28 Technologies, USA). Meanwhile, ambient air was injected into OTCs for control treatment of without O3.

For grain yield determination of wheat, seeds of wheat were sown in OTCs with 15 cm per row at a rate of 225 kg ha−1 in the middle of October. The basic properties of local topsoil in OTCs were organic carbon 1.3 g kg−1, total nitrogen 0.73 g kg−1, available phosphorus 67 mg kg−1 and available potassium 157 mg kg−1, respectively. Materials were treated with ambient air (<40 ppb O3, -O3) or elevated O3 (80 ppb, +O3). NO donor sodium nitroprusside (SNP, 200 μM) was sprayed to leaves once every two days during O3 fumigation. Eight OTCs were randomly allocated to the four kinds of treatments, resulting in two replicates for each treatment. Ozone was artificially added to four OTCs which were used to perform O3 treatment to maintain an O3 concentration of 80 ± 10 for 7 h day−1 (10:00–17:00) from anthesis of wheat in the site field experiment (from 1 May to 30 May).

For eco-physiological analyses, seeds of winter wheat were cultured in the plastic pots. The first expanded leaves of 30-day-old seedlings were used in these analyses. Before O3 exposure, wheat plants were sprayed with equal amounts of SNP solution (200 μM, +SNP) or deionized water (-SNP) treatments, respectively. Then, they were fumigated by 160 ppb O3. Wheat seedlings were treated at different time, but collected at the same time to generate samples treated for 0, 1, 3, 5 and 7 h. This strategy of treatment can discount the circadian effect.

2.2. Prediction wheat yield and determination of grain yield by experiment


The ear number per square meter was counted for each treatment, and 20 matured ears of winter wheat were sampled to determine grain number per ear and 1000-grain weight. Yield per square meter were determined based on ear number, grain number per ear and 1000-grain weight. This determination was repeated in two growing years of wheat (2015–2016 and 2016–2017).

2.3. Determination of endogenous NO and nitrate reductase activity

Endogenous NO concentration of the first expanded leaves of 30-day-old seedlings after 160 ppb O3 treatment for 1 h was determined by imaging the NO-specific report (Zhao et al., 2009). The molecular Probes) under confocal microscopy based on the previous report (Zhao et al., 2009). The fluorescence intensity was determined using the Zeiss LSM510 software.

The nitrate reductase (NR) activity was determined following the method of previous report with some modifications (Scheible et al., 1997). About 1 g of leaves fumigated by ozone for 1 h was ground with liquid N2 and then re-suspended in extraction buffer containing 5 mM dithiothreitol, 1 mM EDTA, 10% (v/v) glycerol, 100 mM HEPES-KOH (pH 7.5), 20 mM FAD, 1 mM leupeptin, 0.5 mM phenylmethylsulfonyl fluoride, 5 mM Na2MoO4, 0.1% Triton X-100, and 1% polyvinylpyrrolidone. The supernatant was separated for determination after centrifuging (10,000 g, 20 min, 4 °C). The NR activity was determined by mixing 1 mL supernatant with 5 mL assay buffer (5 mM KNO3, 0.25 mM NADH, and 100 mM HEPES-KOH, pH 7.5). The mixture was incubated at 25 °C for 30 min, and stopped by adding 0.1 M zinc acetate. Then, tubes were adding with 1 mL of 1% (w/v) sulfanilamide in 3 M HCl and 1 mL of 0.02% (v/v) N-(1-naphthyl)-ethylenediamine. After 15 min, the nitrite produced was determined at 520 nm by spectrophotometer (Bio-Rad). The contents of protein in the supernatant were measured according to the method of coomassie brilliant blue (Bradford, 1976).
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