



Diagnosing ozone stress and differential tolerance in rice (*Oryza sativa* L.) with ethylenediurea (EDU)[☆]



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ARTICLE INFO

Article history:

Received 27 March 2017

Received in revised form

12 May 2017

Accepted 17 June 2017

Available online 29 June 2017

Keywords:

Air pollution

Breeding

Cereals

Food security

Global change

Phenotyping

ABSTRACT

Rising tropospheric ozone concentrations in Asia necessitate the breeding of adapted rice varieties to ensure food security. However, breeding requires field-based evaluation of ample plant material, which can be technically challenging or very costly when using ozone fumigation facilities. The chemical ethylenediurea (EDU) has been proposed for estimating the effects of ozone in large-scale field applications, but controlled experiments investigating constitutive effects on rice or its suitability to detect genotypic differences in ozone tolerance are missing. This study comprised a controlled open top chamber experiment with four treatments (i) control (average ozone concentration 16 ppb), (ii) control with EDU application, (iii) ozone stress (average 77 ppb for 7 h daily throughout the season), and (iv) ozone stress with EDU application. Three contrasting rice genotypes were tested, i.e. the tolerant line L81 and the sensitive Nipponbare and BR28. The ozone treatment had significant negative effects on plant growth (height and tillering), stomatal conductance, SPAD value, spectral reflectance indices such as the normalized difference vegetation index (NDVI), lipid peroxidation, as well as biomass and grain yields. These negative effects were more pronounced in the *a priori* sensitive varieties, especially the widely grown Bangladeshi variety BR28, which showed grain yield reductions by 37 percent. EDU application had almost no effects on plants in the absence of ozone, but partly mitigated ozone effects on foliar symptoms, lipid peroxidation, SPAD value, stomatal conductance, several spectral reflectance parameters, panicle number, grain yield, and spikelet sterility. EDU responses were more pronounced in sensitive genotypes than in the tolerant L81. In conclusion, EDU had no constitutive effects on rice and partly offset negative ozone effects, especially in sensitive varieties. It can thus be used to diagnose ozone damage in field grown rice and for distinguishing tolerant (less EDU-responsive) and sensitive (more EDU-responsive) genotypes.

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1. Introduction

Tropospheric ozone (O₃) poses a major emerging threat to global crop production due to its high phytotoxicity (Tai et al., 2014; Agathokleous et al., 2015a; Ainsworth, 2016). It is one of the most widespread secondary air pollutants, formed through photochemical reactions of precursor gases such as nitrous oxides,

volatile organic compounds, carbon monoxide and methane (The Royal Society, 2008; Paoletti et al., 2014). Detrimental effects of current ambient ozone levels on vegetation including crop growth and yields have been estimated to cause global economic losses in the range of 14–26 billion US\$ (Ashmore, 2005; Feng and Kobayashi, 2009; Van Dingenen et al., 2009; Mills and Harmens, 2011; Avnery et al., 2013). In addition, several model projections predicted that East and South Asian developing countries (including Bangladesh) will be most strongly affected by tropospheric ozone in the coming decades due to insufficient environmental legislation, rapid economic growth and industrial development (Emberson et al., 2009; Van Dingenen et al., 2009;

[☆] This paper has been recommended for acceptance by Dr. Yong Sik Ok.

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Avnery et al., 2011; Pozzer et al., 2012; IPCC, 2014). Among the ten most populated countries in the world, the change in daily maximum average ozone concentration was the highest (21.3%) in Bangladesh, between 1990 (59.4 ppb) and 2013 (72.0 ppb) (Brauer et al., 2016). This trend occurred due to higher emission of ozone precursor gases (Chakraborty et al., 2015; Brauer et al., 2016) arising from unprecedented increases of motor vehicles, conventional brick-making kilns, and fossil fuels combustion without any regulation, in combination with favorable climatic conditions for ozone formation (Akhtar et al., 2010).

Ozone adversely affects crop productivity directly through oxidative damage to cells and indirectly as a greenhouse gas accelerating global warming (Ainsworth, 2016). Rice is the most important staple food crop in Asia, including Bangladesh (Akhtar et al., 2010; Alexandratos and Bruinsma, 2012), the 4th largest rice growing country globally (FAOSTAT, 2013). An estimated 3.7% of global and more than 10% of regional rice yields are lost due to rising ozone, which will exacerbate in near future with further increases in ozone levels (Ainsworth, 2008; Van Dingenen et al., 2009; Frei, 2015). In South Asia rice is cultivated almost year round with two major seasons, and both growing seasons can overlap with the peak ambient ozone episodes (Frei, 2015). Although no field studies have been done so far to determine ozone impacts on rice production, significant yield reduction of Bangladeshi rice cultivars have been reported in controlled environment systems due to elevated ozone (chronic stress, ozone concentration was 60 and 100 ppb) (Akhtar et al., 2010). Therefore, it is essential to develop an effective and reliable research tool which can be used to quantify ozone impacts in the field and to screen a wide range of genotypes grown in ozone affected developing areas such as Bangladesh.

Three types of experimental systems have been used so far for the quantification of ozone impacts on plants: sun-lit plant growth chambers, open top chambers (OTC) and free air concentration enrichment (FACE) (Frei, 2015; Kobayashi, 2015). Sun-lit plant growth chambers are environmentally controlled chambers in which ozone concentrations can be maintained at desired levels for the purpose of better understanding mechanism of ozone damage (Kobayashi, 2015). OTC were first introduced in the early 1970s by Heagle et al. (1973), and are widely used controlled-environment systems, in which ozone concentrations are maintained at desired levels with artificially generated air blowing ozone into the chambers (Frei, 2015). They have been criticized for causing a 'chamber effect' thereby modifying the ozone impacts by changing the microclimate (especially, temperature, humidity, CO₂ concentration), which can differ from the field conditions (Morgan et al., 2006; Piikki et al., 2008; Kobayashi, 2015). Another promising and more realistic approach is free air concentration enrichment (FACE), a chamber-less system for evaluating plant performance in field conditions (Morgan et al., 2004). Despite that, only few studies have been conducted so far with FACE-ozone systems, for example in the USA for soybean (Morgan et al., 2004) and in China for rice and wheat (Shi et al., 2009; Feng et al., 2011, 2016; Tang et al., 2011). Maintaining FACE experiments is expensive, technically challenging and laborious (Frei, 2015). Therefore, this approach is less suitable for developing countries such as Bangladesh due to lack of reliable electricity and infrastructure facilities (Oksanen et al., 2013; Kobayashi, 2015). FACE also has the limitation that it only compares ambient to elevated ozone levels, but unlike chamber experiments offers no possibility of estimating effects of current ambient ozone levels (Pleijel, 2011).

As an alternative to FACE systems, a synthetic chemical, ethylenediurea (*N*-[2-(2-oxo-1-imidazolidinyl) ethyl]-*N'*-phenylurea, abbreviated as EDU) also termed as antiozonant, has been proposed to evaluate the differential responses of plants and crop species

towards ozone damage (Paoletti et al., 2009; Feng et al., 2010; Manning et al., 2011; Agathokleous et al., 2015b). The EDU protection against ozone injury was first reported in bean plants (Carnahan et al., 1978). However, the actual mode of action and prevention mechanisms of EDU against phytotoxic effects of ozone still remain elusive (Paoletti et al., 2009; Manning et al., 2011). It is suggested that EDU may facilitate the scavenging of detrimental ozone activity through a direct effect on physiological parameters, or by antioxidant-mediated defense reactions (Manning et al., 2011; Pandey et al., 2015). As EDU can be applied flexibly by spraying on plants, it may constitute a convenient tool to screen a large number of rice genotypes in field experiments. However, this approach assumes that EDU has an ozone-specific, but no constitutive effect on plants. With few exceptions (such as a study on clover by Karlsson et al., 1995) most EDU studies have been conducted in ambient ozone conditions without any ozone-free control. Therefore, prior to the use in large scale field experiments, specific EDU doses applied to crops should be validated to mitigate ozone effects, without having any effects on plants in the absence of ozone.

To this end, the current study was designed to test contrasting rice genotypes (two *a priori* ozone sensitive and one ozone-tolerant), and to explore the constitutive effect of EDU in the absence or presence of ozone on physiological parameters, growth and rice yield components. Our specific hypotheses were that (i) EDU will play an important role in protecting ozone-stressed plants against phytotoxicity without any constitutive effect, *i.e.* control plants will not be responsive towards EDU; (ii) ozone sensitive genotypes will be more responsive towards EDU in presence of ozone than the tolerant genotype.

2. Materials and methods

2.1. Plant materials and growth condition

The experiment was carried out in a climate controlled glasshouse near Bonn (Campus Klein-Altendorf, University of Bonn), Germany, from April to October 2016. Three different rice genotypes were used for this study (i) Nipponbare (NB), an ozone sensitive Japanese modern rice variety (Jing et al., 2016) (ii) L81, an ozone tolerant introgression line (Wang et al., 2014), which carries two ozone tolerant quantitative trait loci (QTL) from the *Aus* landrace Kasalath (Frei et al., 2008, 2010) in the genetic background of NB (iii) BRRI dhan28 (BR28), an ozone sensitive and high yielding modern rice variety developed by the Bangladesh Rice Research Institute, which is widely cultivated by Bangladeshi farmers (Akhtar et al., 2010). Seeds were germinated in the dark for 3 d at 28 °C and then transferred to a glasshouse under natural light. Seedlings were placed in a mesh floating on solutions containing 0.5 mM CaCl₂ and 10 μM FeCl₃ until transplantation. Three-week-old seedlings were transplanted into three experimental polders measuring 6 m × 2 m filled with a local clay-silt luvisol soil with 16% clay, 77% silt, 7% sand, 1.2% organic carbon and pH 6.3 (Ueda et al., 2015a). Constant water level of at least 3 cm was maintained from 10 d after transplanting throughout the growth season. The polders were previously sealed with PVC sheets at 50 cm soil depth (Frei et al., 2016) and had been used for flooded rice cultivation in three consecutive years before this experiment. Temperature and relative humidity were measured continuously at 2-min intervals (sensor type 224.401, RAM GmbH Mess-und Regeltechnik, Herrsching, Germany), and CO₂ was measured at 10-min intervals (sensor type GMT 222EONOAON1AOB, Vaisala, Helsinki, Finland), respectively. The average daytime (7.00 h–19.00 h) and nighttime (19.00 h–7.00 h) temperatures were 27.8 °C and 20.6 °C, average relative humidity was 54.5% and 81.8%, respectively. The average

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