



# Assessing the impact of current tropospheric ozone on yield loss and antioxidant defense of six cultivars of rice using ethylenediurea in the lower Gangetic Plains of India

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## Abstract

Climate change influences the current tropospheric ozone (O<sub>3</sub>) budget due to industrialization and urbanization processes. In recent years, the impact of elevated O<sub>3</sub> on crop development and yield loss has emerged as one of the most important environmental issues, particularly in rural and suburban areas of the lower Indo-Gangetic Plains of India. The impact of the current tropospheric ozone (O<sub>3</sub>) on the crop yield, photosynthetic yield, and enzymatic antioxidants of six rice (*Oryza sativa* L.) cultivars (IR 36, MTU 1010, GB 3, Khitish, IET 4786, and Ganga Kaveri) was investigated with and without the application of ethylenediurea (EDU). The results revealed that O<sub>3</sub> stress significantly affected crop yield, photosynthetic yield, and antioxidant enzymes. The findings showed that O<sub>3</sub> toxicity induces oxidative stress biomarkers, i.e., malondialdehyde (MDA) content, and was manifested by increasing the enzymatic antioxidants, i.e., superoxidase dismutase (SOD) and catalase (CAT) in four rice cultivars (IR 36, GB 3, IET 4786, and Ganga Kaveri). At the same time, the results also illustrated that the rice cultivars MTU 1010 and Khitish are more tolerant to O<sub>3</sub> stress as they had less oxidative damage, greater photosynthetic SPAD value, SOD and CAT activities, and lower MDA activity. The results also elucidated that the application of EDU decreased O<sub>3</sub> toxicity in sensitive cultivars of rice by increasing antioxidant defense systems. The current O<sub>3</sub> level is likely to show an additional increase in the near future, and the use of tolerant genotypes of rice may reduce the negative impacts of O<sub>3</sub> on rice production.

**Keywords** Ambient ozone · Boro rice · Ethylenediurea · Antioxidants · Photosynthetic yield

## Introduction

Ambient ozone (O<sub>3</sub>), a gaseous pollutant, has assumed a much larger, more intense, and global significance, affecting crop production in many agricultural regions in changing

climate scenarios. O<sub>3</sub> concentrations depend sensitively upon weather variables, and the primary factors influencing their formation are the intensity of solar radiation and the rise in ambient temperature (Gaur et al. 2014; Tiwari et al. 2008; Xu et al. 2016). Changes in regional O<sub>3</sub> levels not only depend upon weather variables but also upon the transportation of O<sub>3</sub> from one region to another along with the prevailing winds. Subtropical climatic conditions prevalent in the South Asia region provide favorable conditions for O<sub>3</sub> formation due to warm and sunny days in the presence of O<sub>3</sub> precursors (Ramanathan and Ramana 2005; Tiwari et al. 2008) due to industrialization and urbanization processes.

High ambient O<sub>3</sub> is highly reactive, and a strong oxidant acts as a phytotoxicant upon entering the plant, affecting metabolism, reducing chlorophyll content, modifying leaf senescence, and decreasing biomass accumulation, resulting in crop yield reduction (Ainsworth et al. 2012; Avnery et al. 2011; Mishra et al. 2013; Fahad et al. 2013; Rai and Agarwal 2015). Significant yield reductions of agricultural

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crops have been well documented due to rising ambient O<sub>3</sub> (Cotrozzi et al. 2016; Rai et al. 2010; Yi et al. 2016). In India, the estimated O<sub>3</sub>-induced yield loss for rice was ~6%, and wheat was ~21% (Sharma et al. 2019), whereas Lin et al. (2018) estimated rice yield loss of 3.9–15.0%, 8.5–14.0% for winter wheat, and 2.2–5.5% for maize in China. Mills et al. (2018) calculated that O<sub>3</sub>-induced wheat yield losses ranged from 7.3 to 8.9% in Germany, France, and Italy. In the USA, O<sub>3</sub>-induced yield losses for wheat and soybean were 4.9% and 6.7%, respectively (Lapina et al. 2016). Predicted and current O<sub>3</sub> trends may increase the relative crop production losses in rice, wheat, soybeans, beans, barley, maize, and potatoes in the near future (Emberson et al. 2009; Feng and Kobayashi 2009).

*Boro* rice is dry-season rice grown in low-lying areas or on medium lands with irrigation after the harvest of wet season rice. The rapid expansion of *Boro* rice cultivation has taken place in recent years in Eastern India (Uttar Pradesh, Bihar, West Bengal, Assam, Odisha, and Andhra Pradesh) and the river basin deltas of Bangladesh. In 2019–2020, the total production of rice in India was 118 million tonnes, of which *Boro* rice accounted for ~14% (DAC 2021). In the neighboring country of Bangladesh, out of 36.4 million tonnes of rice produced in 2019–2020, the share of *Boro* rice was about 54% (IFPRI 2020). The crop is known for its high productivity (5–6 t/ha) in areas where rice productivity has traditionally been poor (2–3 t/ha) during the wet season. Low winter temperatures during early crop growth promote photosynthate accumulation, increasing the carbon–nitrogen ratio (Singh 2002). *Boro* rice is transplanted during December–January and harvested in the hot and humid months of April–May. The total O<sub>3</sub> concentration increases during winter and pre-monsoon periods due to the rise in temperature in changing climatic scenarios (Lu et al. 2019; Ramanathan and Ramana 2005; Tiwari et al. 2008). Ozone concentrations below 40 ppb usually do not influence crop yield, though this threshold value (AOT40) often exceeds as high as ~67 ppb due to the rise in temperature during the *Boro* rice cultivation season (Dey et al. 2014; Ganguly 2012; Singh et al. 2021). Elevated O<sub>3</sub> levels coincide with the late vegetative and reproductive stages such as flowering and grain filling. Rice has been found moderately sensitive to O<sub>3</sub> as other ozone-sensitive crops like wheat and soybean grown during November–May in Southeast Asia, and the O<sub>3</sub>-affected rice crops have lower yields with poor quality grains (Mills et al. 2007; Feng and Kobayashi 2009; Wang et al. 2012; Liu et al. 2015). It has been predicted that by 2050, large stretches of rice crops will be affected by O<sub>3</sub> toxicity, especially in parts of Asia, the Middle East, Africa, and South America (IPCC 2014).

Plants have a diverse spectrum of metabolic reactions at the biochemical level that help them to cope with oxidative stress caused by O<sub>3</sub>. Because of the oxidative nature of O<sub>3</sub>, it

penetrates the plant leaf through stomata and dissolves in the aqueous phase of the sub-stomatal cavity and generates reactive oxygen species (ROS) (Tiwari 2018; Grulke and Heath 2019). ROS can harm proteins, lipids, and nucleic acids, as well as plants (Del and Carrasco 2004; Ishida et al. 1999; Mudd 1996). Enzymatic and nonenzymatic antioxidants such as superoxide dismutase (SOD), catalase (CAT), malondialdehyde (MDA), and other substances help plants to reduce the negative effects of ROS (Afzal et al. 2020; Caregnto et al. 2013; Gratão et al. 2005; Mittler et al. 2004; Sharma et al. 2012; Yadav et al. 2014; Fahad et al. 2017). The activities of SOD and CAT are amplified when exposed to elevated O<sub>3</sub> levels (Liu et al. 2015; Pandey et al. 2015; Ueda et al. 2013).

The protection of sensitive crops from high ambient O<sub>3</sub> could be mitigated in two ways, i.e., either by the application of chemical protectants or by the selection of ozone-tolerant cultivars (Didyk and Blum 2011). A large number of chemicals have been evaluated for the protection of crops from ozone injury, but their application in crop fields is not cost-effective (Archambault et al. 2000). Hence, future agricultural productivity may be dependent on the use of O<sub>3</sub>-tolerant cultivars or the development of O<sub>3</sub>-resistant cultivars that can thrive under elevated ambient O<sub>3</sub> levels (Frei 2015). Farmers may choose more tolerant varieties in the long run to reduce crop losses. Application of EDU has been recommended as a useful research tool to estimate crop losses, especially in rural and semi-urban areas where research infrastructure is the limiting factor (Feng et al. 2010; Manning et al. 2011; Paoletti et al. 2009; Rai et al. 2015; Singh et al. 2010; Tiwari et al. 2005). EDU has no influence on plant growth (Foster et al. 1983; Szantoi et al. 2007) and can better reveal the differences among the cultivars (Oksanen et al. 2013) when screening tolerant cultivars in areas with high concentrations of O<sub>3</sub> (Singh and Agrawal 2017). The present study was conducted with the objective to screen six *Boro* rice cultivars for their O<sub>3</sub> sensitivity or tolerance in terms of growth, biochemical, and yield characteristics. These six varieties of *Boro* rice have been chosen for the study as they are commonly grown in the eastern Gangetic plains during January–May. EDU treatment was used to protect the rice plant from ozone effects. To our knowledge, no such studies involving *Boro* rice cultivars have been carried out in the eastern Gangetic plains of India and Bangladesh to reveal the rice production losses from the risk of ozone-induced damage in field conditions.

## Materials and methods

### The study area and experimental details

During the years 2019 and 2020, field experiments were conducted at two different locations (semi-urban and rural)

in West Bengal (India), namely, Nilganj, a semi-urban site (longitude: 88° 26' E, latitude: 22° 45' N, altitude: 9 m asl), and Bhabanipur village, a rural site, (longitude: 88° 34' E, latitude: 22° 55' N, altitude: 12 m asl). The mean annual rainfall in the study area was in the range of 1100 to 1200 mm with a maximum temperature of 34.0 °C in May and a minimum of 10.0 °C in January. The soil of the study area was moderately alkaline, with a pH ranging from 7.54 to 7.70. The texture is loam and sandy loam having 2.3 to 6.0 g/kg organic carbon, 26 to 117 kg/ha available Bray's phosphorus (P<sub>2</sub>O<sub>5</sub>), and 29 to 62 kg/ha ammonium acetate exchangeable potassium (K).

At each location, field plots of 400 m<sup>2</sup> with three replications were established. Six varieties of rice (IR 36, MTU 1010, GB 3, Kshitish, IET 4786, and Ganga Kaveri) were collected from ICAR-NRRI (Cuttack, India) and grown during the *Boro* season (January–April). Rice was transplanted as seedlings following the system of rice intensification (SRI) method. The manure and chemical fertilizer application rates were based on the initial soil test value and percentages of the recommended doses for the crop (N:P:K: 80:40:40 kg/ha). Crops were managed by optimizing plant densities, split N fertilization, timely weeding, and plant protection measures.

### Use of ethylenediurea as antiozonant

EDU, an antiozonant chemical [N-(2-2-oxo-1-imidazolidinyl) ethyl-N-phenyl urea], has emerged as an effective research tool for evaluating O<sub>3</sub> injury in plants (Agathokleous et al. 2016a; Carnahan et al. 1978; Manning et al. 2011; Singh et al. 2015). EDU does not enter the cell but remains confined to the foliar apoplastic spaces and hence is systemic in nature (Pasqualini et al. 2016; Paoletti et al. 2009). Its retention time in the leaf varies from 8 to 21 days, depending upon the soil fertility conditions (Agathokleous et al. 2016b). As such, repeated application of EDU is recommended for the treatment to be effective.

Both experimental sites were divided into two parts, i.e., one as ambient O<sub>3</sub> and the other as EDU treatment plots. Each part had 18 subplots (2 m × 1 m in dimension) for each cultivar. EDU was applied at a concentration of 300 ppm to each plant as a foliar spray until the entire foliage was visibly saturated. The selection of EDU concentration (300 ppm) was based on the earlier study, suggesting that 200–400 ppm of EDU would be the most effective concentration in protecting agricultural plants against O<sub>3</sub> stress (Feng et al. 2010; Pandey et al. 2015). In the ambient O<sub>3</sub> plots, water was sprayed in place of EDU. To prevent the spread of EDU to control plots, there was 2 m spacing between ambient O<sub>3</sub> and EDU-treated plots. The EDU treatment was started 30 days after the transplanting (DAT) of rice seedlings, and 6

numbers of EDU spraying were done at intervals of 15 days until the final harvest (Pandey et al. 2015).

### Ozone monitoring and crop yield

Ambient O<sub>3</sub> concentrations were monitored using the 2B Tech O<sub>3</sub> Monitor (POM) for 6 h per day (10:00 to 16:00 h), regularly at both the experimental sites throughout the growing season (February to May). These experimental locations were not exposed to any direct emissions from air pollution sources.

As described by De Leeuw and Van Zantvoort (1997), AOT40 (accumulated exposure over a threshold of 40 ppb) was used as the exposure index for the O<sub>3</sub> concentration. AOT40 is an exposure-plant response index function set by the United Nations Economic Commission for Europe (UNECE) and US-EPA. It is calculated as the sum of differences between the hourly O<sub>3</sub> concentration and the threshold value of 40 ppb for each hour when the averaged O<sub>3</sub> concentration exceeds 40 ppb. It is expressed mathematically as,

$$AOT40 = \sum_{i=1}^n ([O_3] - 40)_i \text{ for } [O_3] > 40\text{ppb}$$

where [O<sub>3</sub>] = hourly averaged O<sub>3</sub> concentration; 40 = threshold value of O<sub>3</sub>.

An AOT40 value of 10,000 ppb h for daylight hours (radiation > 50 W/m<sup>2</sup>) over a 6-month period has been established as a critical level for the protection of forests. While for the protection of agricultural crops from a 5% loss in yield, an AOT40 value of 3000 ppb h for daylight hours over a growing season has been established as the critical level (WHO 1996; Beck et al. 1998).

Final harvesting was carried out as per the crop duration of each variety (110–125 days). Harvest parameters such as grain weight (after threshing) were measured for all plants in each plot for both the EDU and the ambient O<sub>3</sub>-exposed plants within each cultivar and each treatment. Relative yield loss (RYL) calculation of rice based on AOT40 values was done using crop yield data from the EDU-treated plant yield that had resulted without O<sub>3</sub>-induced damages as per the following equation (Sinha et al. 2015).

$$RYL = -0.00001 \times AOT40 + 0.95 \text{ (Indian rice cultivars)}$$

### Biomass sampling and biochemical measurements

Plant sampling for biochemical analysis of superoxide dismutase (SOD), catalase (CAT), and lipid peroxidation (MDA) was performed at two phases, i.e., the vegetative phase and the maturity phase, as per the crop duration of each cultivar of rice. The samples were taken from the youngest fully mature leaves of five randomly selected

plants within each cultivar of each treatment. The leaf samples were immediately frozen in liquid nitrogen and stored at  $-20\text{ }^{\circ}\text{C}$  until further analysis.

SOD activity was assayed using the photochemical nitroblue tetrazolium (NBT) method (Dhindsa et al. 1981). Fresh leaves (250 mg) were homogenized in liquid nitrogen and 3 mL of 50 mM sodium phosphate buffer (pH 7.8), including 1.5 mM EDTA and 1.0 mM ascorbic acid. SOD activity was measured in 5 mL reaction mixture containing 50 mM sodium phosphate buffer (pH 7.8), 75 mM NBT, 0.5 mM riboflavin, 13 mM methionine, 0.1 mM EDTA, and enzyme extract. Finally, the sample was measured by using a UV–VIS spectrophotometer at 560 nm. CAT activity was assayed by following the decrease in absorbance at 240 nm as  $\text{H}_2\text{O}_2$  was consumed (Aebi 1984). Fresh leaves (250 mg) were homogenized in liquid nitrogen and 3 mL of 50 mM potassium phosphate buffer (pH 7.0). The assay mixture (3.0 mL) was comprised of 75 mM  $\text{H}_2\text{O}_2$ , 100 mM phosphate buffer, and enzyme extract. The CAT activity was measured at a 240 nm wavelength using a UV–VIS spectrophotometer.

The degree of lipid peroxidation was measured as malondialdehyde (MDA) content by the thiobarbituric (TBA) acid method (Heath and Packer 1968). Briefly, 250 mg of frozen leaves were ground at  $4\text{ }^{\circ}\text{C}$  in a mortar with 4 mL of 0.1% trichloroacetic acid (TCA) solution. The homogenate was centrifuged at 15,000 rpm at  $4\text{ }^{\circ}\text{C}$  for 10 min. A total of 1 mL of supernatant was mixed with 4 mL of 0.5% TBA. The mixtures were heated at  $95\text{ }^{\circ}\text{C}$  for 10–15 min and then quickly cooled in an ice bath. The absorbance of the supernatant was recorded by using a UV–VIS spectrophotometer at wavelengths of 532 and 600 nm.

Chlorophyll content in terms of SPAD value was measured using the Leaf CHL PLUS chlorophyll meter. The

SPAD value is related to the amount of chlorophyll present in the leaf between wavelengths of 650 and 940 nm.

## Data analysis

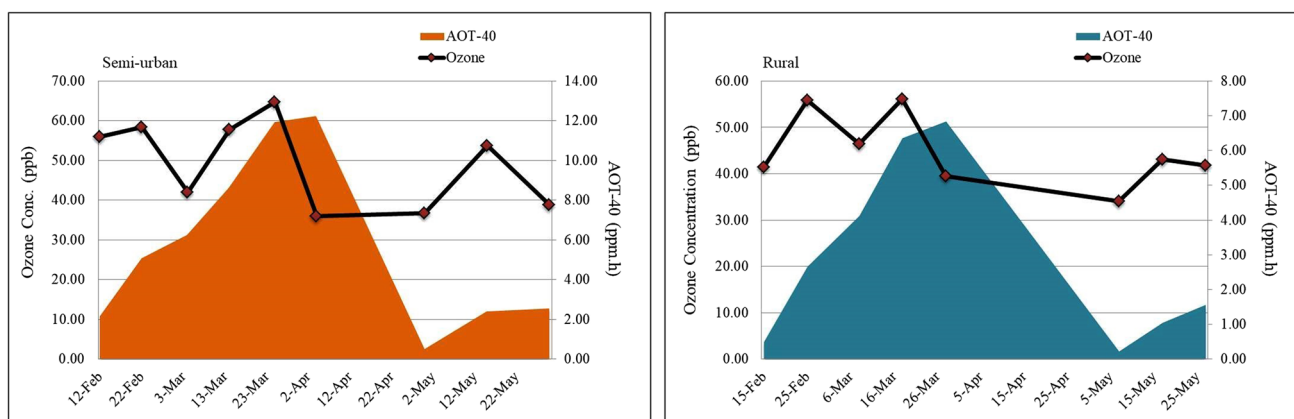
Data recorded in the 2019 and 2020 cropping seasons was pooled together on the account of nonsignificant interaction between years, locations, and treatments. The data was then subjected to ANOVA for each year of sampling. The average value of treatments was separated using the least significant difference (LSD) at the 0.05 probability level.

## Results

### Ozone exposure and yield loss

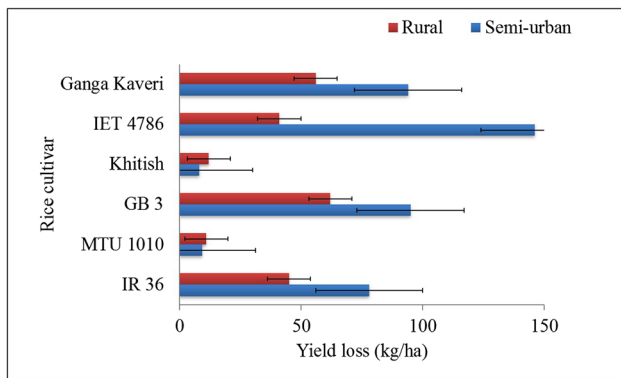
Ozone formation was high during the months of February to May due to long hours of sunlight and a daily increase in ambient temperatures, which speed up the  $\text{O}_3$ -forming photochemical reactions. The trends in ambient  $\text{O}_3$  concentrations were higher than the threshold value of 40 ppb (AOT40) in both semi-urban and rural areas during both years (2019 and 2020). Daytime  $\text{O}_3$  levels often exceeded 40 ppb during the early vegetative phase of rice plants (40 DAT) and attained maximum levels in the reproductive phase (70 DAT). However, accumulated ozone exposure (AOT40) was significantly lower in rural areas as compared to semi-urban areas (Fig. 1). Maximum AOT40 exposure was 12.23 ppm.h in semi-urban areas and 6.83 ppm.h in rural areas.

The results of the final harvest showed a significant relative yield loss in IR 36, GB 3, IET 4786, and Ganga Kaveri cultivars of *Boro* rice under tropospheric  $\text{O}_3$ -treated plants



**Fig. 1** This line graph depicts the seasonal variation in the concentration of tropospheric ozone in the *Boro* rice-growing season in semi-urban and rural areas (February–May). The primary  $x$ -axis indicates the tropospheric ozone concentration in parts per billion (ppb) at an interval of 10 days. The secondary  $x$ -axis indicates the AOT40 value

(accumulated exposure over a threshold of 40 ppb per hour during the crop growing period) in parts per billion (ppm.h). (For the interpretation of the references to color in this figure legend, the reader is referred to the web version of this article)



**Fig. 2** Relative crop yield loss in *Boro* rice cultivars under ambient  $O_3$  in rural and semi-urban areas (mean value of 2-year data,  $p < 0.05$ )

(control) at both locations (Fig. 2). There was no significant yield difference in MTU 1010 and Khitish cultivar for EDU and control treatments at both sites of experiments and may be considered well-adapted cultivars for high ozone exposure. All the yield-related parameters showed more decline in the control plots, which might be due to higher tropospheric  $O_3$  levels between the vegetative and maturity phases. Rice production losses due to tropospheric  $O_3$  exposure were estimated to be 8–11%, using an equation derived from Indian studies. The yield loss was roughly 47% lower in rural areas (37.83 kg/ha), where the AOT40 value was significantly lower than in semi-urban areas (71.72 kg/ha). Ozone exposure-crop yield relationships

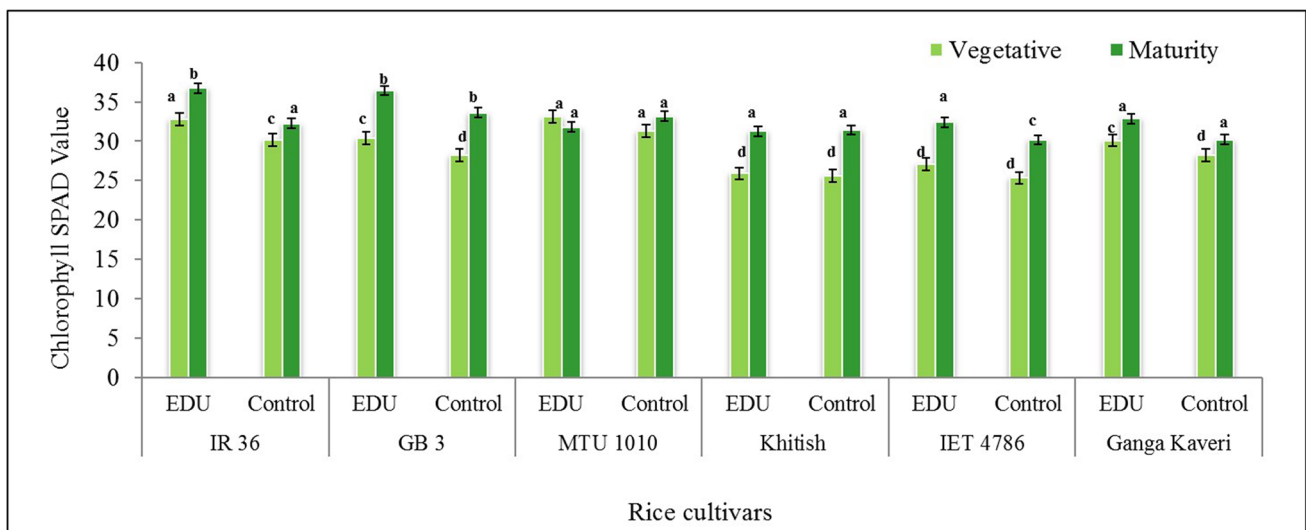
showed significantly lower relative yields, which may be attributed to the variety of cultivars more sensitive to  $O_3$  exposure.

### Photosynthetic yield of the plants

Chlorophyll content plays an important role in determining the photosynthetic yield of the plants. Chlorophyll SPAD values of rice leaves were found significantly higher in EDU-treated plants (Fig. 3). Chlorophyll content was more affected in higher AOT40 areas (semi-urban). Higher AOT40 may prevent chlorophyll synthesis, leading to a decline in SPAD value. At the vegetative phase, the SPAD value was significantly lower as compared to the maturity phase in both EDU and control treatments. SPAD values in MTU 1010 and Khitish cultivars were nonsignificant in both treatments at the vegetative and maturity growth stages (Fig. 3).

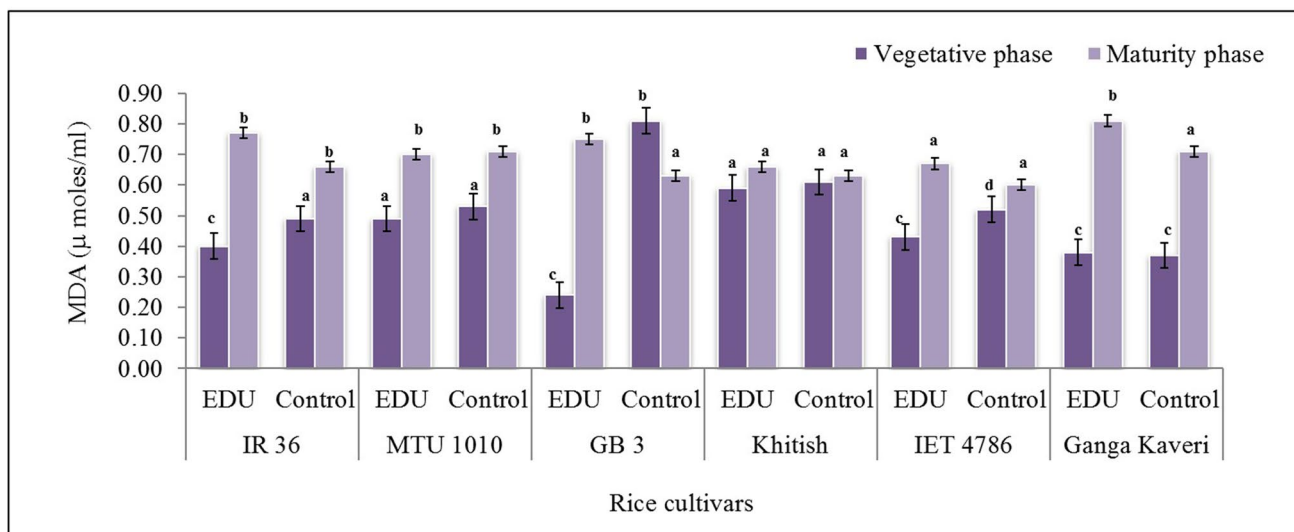
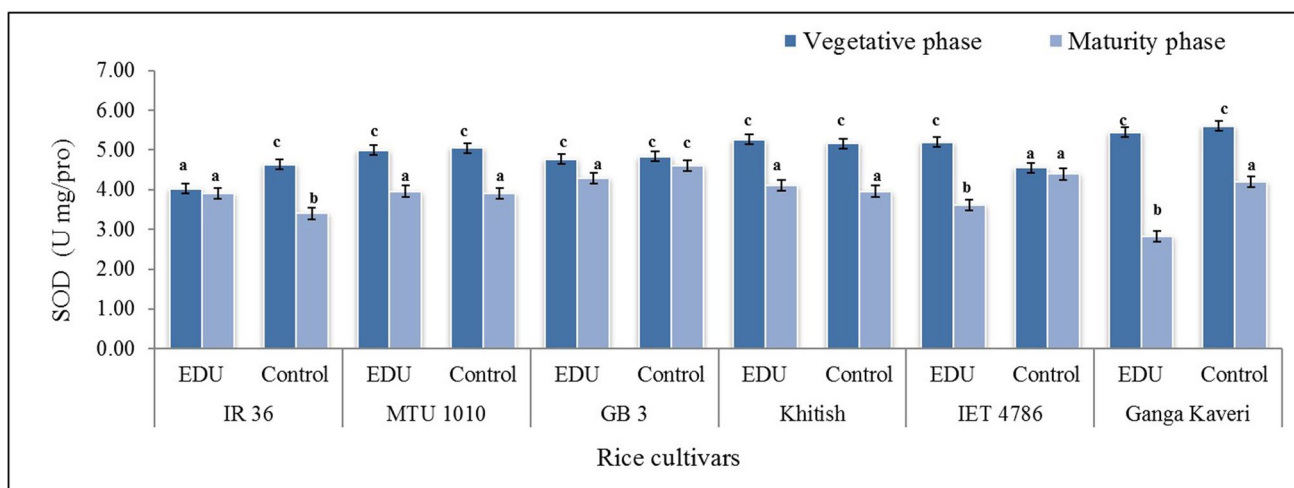
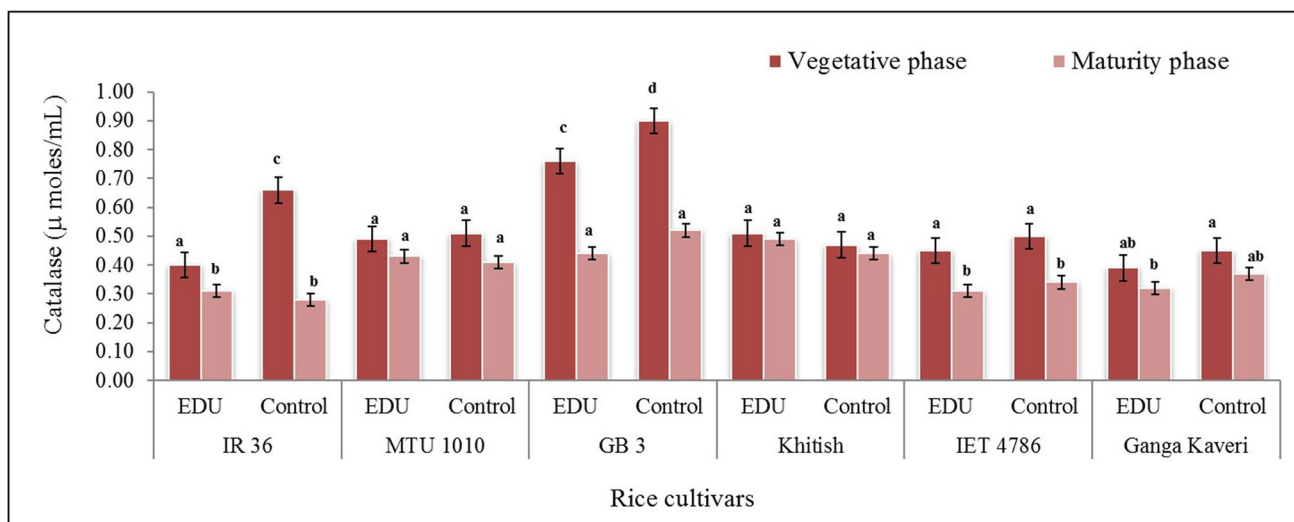
### Effect on the antioxidant pool

Plants possess a wide range of responses at the biochemical level that assist them in coping with  $O_3$ -induced oxidative stress. The antioxidative defense was elevated in response to EDU in all cultivars but varied between the developmental phases of rice plants. An increase in CAT activity at the vegetative phase (0.44–0.76  $\mu$  mol/ml) suggests increased stress on all rice cultivars (Fig. 4a). Reduced CAT activity at the maturity phase (0.31–0.49  $\mu$  mol/ml) may be associated with the exhaustion of the antioxidant defense system after high  $O_3$  stress. Increased



**Fig. 3** Mean chlorophyll SPAD value in rice plants at semi-urban and rural sites of the experiment (mean value of 2 years of data from both study sites. Bars with different letters for each cultivar differ significantly from one other ( $p < 0.05$ )). All the data represented the average of three replications of each cultivar at each site

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SOD activity was also recorded at the vegetative phase (4.02–5.44 U mg/pro) with a decline at the maturity phase (3.9–4.39 U mg/pro) (Fig. 4b). The reduction in

lipid peroxidation (MDA) content (0.24–0.59 μ mol/ml) in all rice cultivars during the vegetative phase indicates that cell membranes are highly sensitive to ozone damage

**Fig. 4 a** Response of catalase (CAT) in different cultivars of rice during the vegetative and maturity phases (mean value of 2-year data from both study sites). Bars with different letters for each cultivar differ significantly from one other ( $p < 0.05$ ). All the data represented the average of three replications of each cultivar at each site. **b** Response of superoxide dismutase (SOD) in different cultivars of rice during the vegetative and maturity phases (mean value of 2-year data from both study sites). Bars with different letters for each cultivar differ significantly from one other ( $p < 0.05$ ). All the data represented the average of three replications of each cultivar at each site. **c** Response of reduced lipid peroxidation (MDA) in different cultivars of rice during the vegetative and maturity phases (mean value of 2 year data from both study sites). Bars with different letters for each cultivar differ significantly from one other ( $p < 0.05$ ). All the data represented the average of three replications of each cultivar at each site

(Fig. 4c). In MTU 1010 and Khitish cultivars of rice, the values of CAT, SOD, and MDA were found nonsignificant between EDU and control treatments at both the vegetative and maturity phases.

## Discussion

The  $O_3$  concentration at a rural and semi-urban site clearly showed sharp monthly variations. The rise in  $O_3$  concentrations during March and May can be attributed to its linear relationship with the increase in solar radiation (Han et al. 2011). Low  $O_3$  levels were observed during the month of April due to cloudy days and pre-monsoon rain that reduced the availability of precursors for the production of  $O_3$  (Tiwari and Agrawal 2018).  $O_3$  precursors such as carbon monoxide (CO), volatile organic compounds (VOCs), and nitrogen oxides (NO<sub>x</sub>) are major contributors to  $O_3$  production. It was observed that total  $O_3$  concentration was much higher in semi-urban areas than in rural areas due to increases in industrial activity as well as a large increase in the number of vehicles (Kurokawa et al. 2013). Several studies suggest that reductions in the emissions of  $O_3$  precursors are the main reason for the decreasing trend of  $O_3$  (Butler et al. 2011; Monks et al. 2015; Hogrefe et al. 2011).

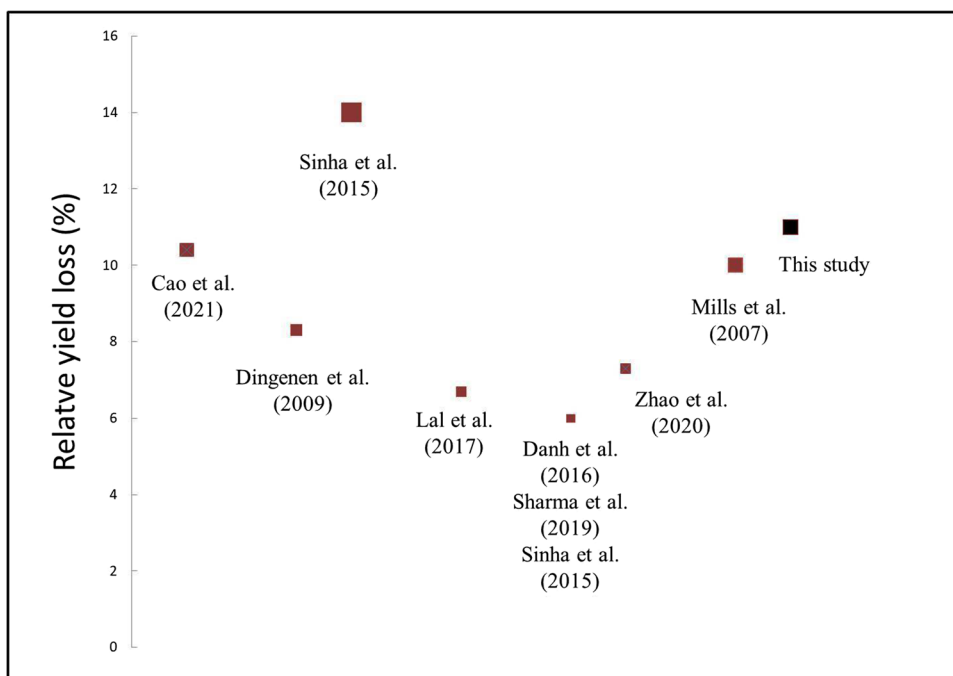
*Boro* rice plants were exposed to very high  $O_3$  concentrations (> 50 ppb), particularly during the vegetative and reproductive phases (February–March). These  $O_3$  concentrations are in line with several other measurements in the IGP region of India (Deb Roy et al. 2009; Oksanen et al. 2013; Singh et al. 2010). Atmospheric  $O_3$  above the threshold value (> 40 ppb) has the potential to damage plant tissues, accelerate leaf senescence, and alter nitrogen cycling in plant ecosystems, which thereby influences plant growth and biomass production (Pandey et al. 2015; Singh and Agrawal 2017). The AOT40 indices at both sites exceeded the critical limit of 3 ppm.h for cereal plants (Mills et al. 2007; Rai et al. 2010). RYL values based on the AOT40

index were in the range of 41 to 147 kg/ha. The maximum area of *Boro* rice in India is in the eastern region (~ 2.32 million ha) followed by the southern (~ 1.42 million ha) and northern regions (~ 0.10 million ha). Due to the high concentration of tropospheric  $O_3$  in the eastern region of India, the total *Boro* rice crop loss per annum may be in the range of 0.56 to 0.78 million metric tonnes (8–11%) if  $O_3$ -resistant cultivars of rice are not grown. This loss in rice production could be about 83.75 million USD. Again, it is very explicit that the loss estimated using the AOT40 metrics is much higher in the neighboring country Bangladesh (~ 2.1 million metric tonnes) from the 4.77 million hectare area of *Boro* rice. Similar results on rice yield loss caused by  $O_3$  from all over the world have been reported (Cao et al. 2020; Dingenen et al. 2009; Danh et al. 2016; Mills et al. 2007; Pandey et al. 2015; Singh and Agrawal 2017; Zhao et al. 2020). The yield loss for rice is significantly higher in India (Fig. 5), while in the other regions, it is less than 5% (Lal et al. 2017; Sinha et al. 2015; Sharma et al. 2019). Two highly responsive cultivars of rice, i.e., MTU 1010 and Khitish, had a grain yield per plot higher than the mean grain yield in both rural and semi-urban areas and have the potential to sustain the attainable yield in unfavorable tropospheric  $O_3$  concentration. The varietal details of the six rice cultivars used in this study are given in Table 1. The difference in crop duration of all the rice varieties was only 10–15 days at the harvesting stage.

ROS produced due to high  $O_3$  concentration affected the chloroplasts formation, leading to the destruction of photosynthetic pigments (Rai and Agrawal 2014), and thus a reduction in the chlorophyll SPAD value of  $O_3$  susceptible cultivars of rice plants during the vegetative phase. Similar results were observed in  $O_3$  susceptible plants in several studies (Kollner and Krause 2003; Pellegrini 2014; Singh et al. 2009), which may be considered indicative of  $O_3$  stress on chlorophyll-binding proteins. The destruction of plant cells was higher during early vegetative stages when the defense mechanisms were insufficient to scavenge the produced ROS. During the later stages, plants were acclimatized to  $O_3$  stress conditions and loss of chlorophyll was minimized (Singh et al. 2009).

Most of the responses in biochemical parameters related to oxidative stress and antioxidative defense varied between the rice cultivars. The response of the plant defense system to  $O_3$  stress varies with the time and duration of high  $O_3$  contact and plant developmental stage. ROS operates as an indicator molecule for initiating protective responses at a specific threshold, with  $H_2O_2$  acting as a secondary messenger. As a result, antioxidant enzymes such as CAT and SOD work together to detoxify ROS (Gill and Tuteja 2010; Suzuki et al. 2012). Antioxidant enzymes in the tolerant cultivar alleviated the stressful condition by inhibiting stress impact by protecting ROS formation. In this study, we observed that

**Fig. 5** Relative yield loss (%) in rice as per the AOT40 index reported from different studies in Asian countries



O<sub>3</sub> stress-induced CAT and SOD activity were significantly higher in tolerant rice cultivars (MTU 1010 and Khitish), compared to sensitive cultivars, implying a function for CAT and SOD in O<sub>3</sub> tolerance by detoxification of H<sub>2</sub>O<sub>2</sub>. There was an upregulation of MDA content in EDU-treated plants, thereby suggesting low exposure of O<sub>3</sub>. EDU protects the membranes against lipid peroxidation through increased

levels of ROS scavenging enzymes. Plants having high antioxidant levels, either naturally occurring or induced, were found more resistant to oxidative damage (Wang et al. 2013; Singh et al. 2010). The efficacy of the ROS scavenging system to maintain the cellular redox steady state of the leaf tissue was responsible for genotypic differences among all rice cultivars (Castagna and Ranieri 2009; Giacomo et al. 2010).

**Table 1** Varietal details of six rice cultivars tested under a high ambient ozone

Rice cultivar	Varietal characteristics				
	Parentage	Duration (days)	Average yield (ton/ha)	Grain type	Special features
MTU 1010 (IET 15,644)	Krishnaveni/IR 64	110–120	4.0–4.5	Long slender	Semi-dwarf (100 cm), resistant to blast and tolerant to brown plant hopper
Khitish (IET 4094)	BU-1 × CR-115	120–125	4.0–4.5	Long slender	Dwarf (90 cm), resistant to blast and tolerant to rice brown spot (BS)
IR-36	IR 1561–228/1 (IR 244/O.nivera./CR94-13)	120–125	4.0–5.0	Medium bold	Semi-dwarf (100 cm), resistant to brown spot, gall midge, leaf folder, and plant hopper
Shatabdi (IET-4786)	CR 10–114/CR 10–115	120–125	5.0–5.5	Long slender	Dwarf (90–95 cm), tolerant to sheath blight, bacterial leaf blight, and sheath rot
Gontra Bidhan-3 (GB-3)	Selection from farmers’ field	120–125	5.5–6.0	Short medium bold	Semi-dwarf (100 cm), resistant to several pests and disease
Ganga Kaveri (GK 5022)	Hybrid	120–125	4.5–5.0	Long slender	Semi-dwarf (105 cm), resistant to leaf blast and brown plant hopper



## Conclusions

Ozone in the troposphere is a serious problem of concern due to its phytotoxicity, limiting crop productivity worldwide. Rice plants show a wide range of responses to higher concentrations of O<sub>3</sub>, which are mostly manifested by a variety of alterations in the chlorophyll content, biochemical attributes, antioxidant enzyme activities, and economic yield. Although high O<sub>3</sub> concentrations may cause negative effects on the overall growth and development of the rice plants, the vegetative and reproductive phases are the most affected. Other noticeable effects of O<sub>3</sub> stresses were damaged photosynthetic machinery and oxidative damage in sensitive cultivars of rice. Recent advances have been made in reducing the detrimental consequences of ozone stress, either through genetic methods or stress resistance induction. In this study, two O<sub>3</sub>-tolerant rice cultivars had less oxidative damage and showed higher levels of photosynthetic SPAD value, SOD and CAT activities, and a lower level of MDA activity as compared to O<sub>3</sub>-sensitive cultivars. In view of the rising tropospheric O<sub>3</sub> problem, emphasis needs to be given to developing O<sub>3</sub>-resistant cultivars either through conventional breeding methods or through the utilization of biotechnological tools to reduce the impact of O<sub>3</sub> on staple food crops like rice to ensure food security under changing climatic scenarios. Cultivation of O<sub>3</sub>-tolerant rice cultivars may help in reducing the detrimental environmental effects associated with increased levels of O<sub>3</sub>. The findings also demonstrated the utility of EDU as a technique for monitoring cultivar-specific sensitivity to ambient O<sub>3</sub> and suggested that it may be used more regularly, particularly in rural and semi-urban locations where research infrastructure is limited.

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**Data availability** The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Ethics approval and consent to participate** We all declare that manuscript reporting studies do not involve any human participants, human data, or human tissue. So, it is not applicable.

**Consent for publication** Our manuscript does not contain any data from any individual person, so it is “not applicable.”

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