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Effects of elevated CO_2 concentration on water productivity and antioxidant enzyme activities of rice (*Oryza sativa* L.) under water deficit stress

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ABSTRACT

Rice is the foremost staple food in India, safeguarding the food security of the country. Rising levels of atmospheric CO_2 concentration affect water productivity and antioxidant enzyme activities of rice, yet the interactive effects of elevated CO_2 (ECO_2) and water deficit stress (WDS) on rice has remained unclear. The present experiment was conducted for two years under Open Top Chambers (OTCs) to elucidate the effects of ambient CO_2 (400 ± 10 μmol mol^{-1}) and two levels of ECO_2 (550 ± 20 μmol mol^{-1} and 700 ± 20 μmol mol^{-1}) under well watered condition (WW) and water deficit stressed to −60 kPa on water productivity (Wp) and antioxidant enzyme activities in rice. In water deficit treatments, measured amount of water was applied as surface irrigation, each time the soil water potential as measured by tensiometers, reached −60 kPa. The results showed that ECO_2 increased the growth and yield characteristics, e.g., leaf area index and productive tillers, resulting in an increase in grain and straw yield under both WW and WDS. The increased concentration of antioxidant enzymes like proline, catalase and peroxidase under ECO_2 helped the plant to combat the adverse effects of WDS. Under ECO_2, there was a decrease in irrigation water input by 5–14%, resulting in increase in water productivity (Wp) by 35–49% under different water regimes. ECO_2 had positive effect on plant height, productive tillers, grain and straw yields even under WDS because the temperature at our study site did not increase beyond 33 °C during rice reproductive phase. Our data provides an opportunity to test theoretical models for evaluating rice production under climate change scenario.

1. Introduction

Rice is an excessive user of water and is sensitive to water deficit stress (WDS) with reductions in yield at different levels of WDS (Bouman et al., 2006; Yang et al., 2007; Ghosh and Singh, 2010; Dasgupta et al., 2015; Kumar et al., 2016). The present atmospheric CO_2 concentration is about 400 μmol mol^{-1} (http://CO2.now.org) and is projected to surpass 550 ± 20 μmol mol^{-1} by the middle; and 700 ± 20 μmol mol^{-1} by the end of the 21 st century (IPCC, 2013; Solomon et al., 2007). Increasing atmospheric CO_2 concentration results in elevated mean global temperature (Houghton, 2001) leading to climate change with increased risks of flood and drought (Bates et al., 2008). Elevated CO_2 (ECO_2) decreases transpiration (Baker and Allen, 2005) and increases canopy photosynthesis (Widodo et al., 2003), plant growth and grain yield (Roy et al., 2012). Thus, increased atmospheric CO_2 may reduce the impact of WDS on rice production. Keeping in mind, the economic importance of this crop, studies on the interaction of ECO_2, temperature rise and water deficit stress on rice agronomic and physiological parameters are urgently needed.

The effect of high atmospheric CO_2 concentration on growth and different physiological activities is greater on C_3 plants as compared to C_4 plants (Gifford, 1992; Ghannoum et al., 2000; Griffin et al., 2000; Gunderson et al., 2000; Jach and Ceulemans, 2000; Watling et al., 2000; Hymus et al., 2001). Being a C_3 plant, rice is more sensitive to the changes in the atmospheric CO_2 (Cheng et al., 2010). A yield advantage of 23% was observed when CO_2 concentration was increased from 390 to 550 μmol mol^{-1} under open top chambers (OTC) (Roy et al., 2012). Similar increase in grain yield was also observed in rice by Sasaki et al., 2007; Ma et al., 2007., Jia et al., 2015. There are contradictory reports on the effects of ECO_2 on yield of rice varying from decrease in yield (Satapathy et al., 2015) to yield increase (Roy et al., 2012, 2015; Madan et al., 2012; Bhattacharyya et al., 2013). The increase in concentration of atmospheric CO_2 and other greenhouse gases is expected to increase the global air temperature by 0.5 °C in the last century and is estimated to continue increasing by 1.4 − 5.8 °C by the end of 21st century (Houghton, 2001). This anticipated increase in temperature would

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affect the precipitation balance, likely increasing the severity of crop water deficit (IPCC, 2007). This has consequences for rice production, since yield loss of rice caused by WDS is enormous (Wopereis et al., 1996; Dasgupta et al., 2015; Kumar et al., 2016, 2017). Consequently, it is of high importance to elucidate the effects of ECO_2 and associated temperature rise in conjunction with WDS on rice plants.

Atmospheric CO_2, the main source of carbon for plants, has significant fertilization effects on crops. In order to absorb CO_2, plants have to open their stomata, which is followed by a loss of moisture through transpiration. Under ECO_2 concentration, stomatal opening is reduced and this may result in improved water use efficiency, lower transpiration rate, shortened crop growth period, increased plant height and yield (Long et al., 2004; Ainsworth and Long, 2005; Ainsworth and Rogers, 2007; Wall et al., 2011; Ziska, 2013). Leaf level gas exchange measurements show that ECO_2 significantly ($p \leq 0.05$) increased both canopy net photosynthetic rate (21–27%) and water productivity while decreasing evapotranspiration by about 10% (Baker and Allen, 2005). The formation of reactive oxygen species (ROS) may be alleviated under ECO_2 due to consumption of more electrons in carbon fixation, and hence fewer are channelled into ROS producing pathways, such as photorespiration or the Mehler reaction (Asada, 1999). Qaderi et al. (2006) concluded that physico-chemical modifications arising from ECO_2 concentrations may ameliorate some of the effects of elevated temperature and water deficit stress. Similar suggestions were made by Aranjuelo et al. (2008) and Erice et al. (2007). Researchers have examined the effects of ECO_2 and WDS on the growth and water use efficiency of C_3 plants like wheat (Qiao et al., 2010) and soyabean (Li et al., 2013).

Dasgupta et al. (2015) reported results of experiment on rice plants that were exposed to WDS treatments under ambient CO_2. Proline accumulation and electrolyte leakage was increased, whereas relative water content was decreased under WDS. Several previous authors (Lum et al., 2014; Maisura Chozin et al., 2014; Kumar et al., 2017) reported changes in plant water status and antioxidant defence metabolite accumulation in rice plants under WDS conditions. In general, plants under WDS produce more antioxidant enzymes (e.g; catalase, peroxidase etc.) to detoxify the reactive oxygen species (ROS), whose production is enhanced under WDS conditions (Lum et al., 2014; Dasgupta et al., 2015; Kumar et al., 2017). The results of the prior studies confirmed that antioxidant stress metabolites were involved in mitigating the effect of WDS on rice plants. All these studies on rice under WDS were conducted under ambient atmospheric CO_2 concentration. However, it is unclear how rice plants under WDS will behave under CO_2 enriched environment. It is very likely that the effect of WDS differs under ambient and enriched CO_2 conditions, and this could change the WDS dependent metabolite response of rice. To understand the effects of a complex future environment on rice production, it is important to study the effects of ECO_2 on plant water status and changes in activity of antioxidant metabolites of rice plant under WDS.

We hypothesized that ECO_2 would reduce the negative effects of WDS by improving plant water relations and increasing the antioxidant metabolite activities in rice. The present study aims to elucidate the combined effects of ECO_2, associated temperature rise and WDS on water productivity, leaf water status and antioxidant metabolite response of rice plant.

2. Materials and methods

2.1. Experimental site description

The study was conducted at the research station of the Central Rice Research Institute (CRRI), Cuttack (20°27′10″N, 85°56′9″E; elevation from mean sea level 24 m) in Eastern India. The site is characterized by tropical climate, short winter, lengthy hot summer and heavy cyclonic rainfall during the monsoon. Three pairs of OTCs with CO_2 enrichment facility were set up in 2009 at CRRI, research station. The system had been operating for 5 years until the beginning of our experiment. Relevant soil properties were as follows: clay (0.002 mm) 26.4%; silt (0.002-0.02 mm) 56.3%; sand (0.02–2 mm) 17.3%; bulk density 1.35 Mg m^{-3}; pH (1:2.5, soil: water suspension) 7.2; electrical Conductivity (using 1:2.5; soil:water suspension) 0.46 dS m^{-1}; cation exchange capacity 14.8 Cmol (P^+) kg^{-1}; organic carbon 0.51%; available N 281 kg ha^{-1}; available P_2O_5 18 kg ha^{-1}; available K_2O 154 kg ha^{-1}; moisture content at field capacity 0.31 cm^3 cm^{-3}; moisture content at permanent wilting point 0.12 cm^3 cm^{-3}; available water capacity 0.19 cm^3 cm^{-3}.

2.2. OTC design and CO_2 concentrations

Six circular shaped OTCs were used for conducting the CO_2 enrichment experiment (diameter 4 m and height 3 m; M/S Neogenesis Engineering, Thane, Maharashtra, India). The OTCs were arranged in the field in a randomized block design with two replications (De Costa et al., 2006; Roy et al., 2012, 2015; Bhattacharyya et al., 2013, 2014, 2016). The OTCs were made up of transparent polycarbonate sheets with about 88–90% transparency. This ensured that light intensity was not a limiting factor for the growth of rice crop inside the OTCs. Considering the present ambient CO_2 and anticipated increase in CO_2 levels in next several decades as per IPCC (2007), three CO_2 levels were considered for the OTC experiments including ambient (400 ± 10 μmol mol^{-1}) and elevated (550 ± 20 μmol mol^{-1}; CC_{500} and 700 ± 20 μmol mol^{-1}; CC_{700}). Two OTCs were assigned for each level of elevated CO_2 (550 ± 20 μmol mol^{-1} and 700 ± 20 μmol mol^{-1}) and the remaining two OTCs were kept under ambient CO_2 (Fig. 1). In total, there were 8 experimental treatments with 2 replications (n = 16) as described in Table 1. The upper portions of the OTCs were kept open to maintain natural condition of temperature and humidity. The maximum and minimum temperatures for all the treatments were monitored using digital thermometer. The details of temperature inside and outside the OTCs for the entire crop growth period are presented as supplementary figure (fig. S1). The air temperature during the cropping season at critical growth stages was not so high (air temperature ranged from 29.1 ± 1.8 to 30.4 ± 1.4 °C and 29.5 ± 0.6 to 32.4 ± 1.1 °C during anthesis to grain filling at ambient and elevated CO_2 respectively) that it could cause a grain yield reduction (Wassmann et al., 2009). The relative humidity (RH) varied in the range of 47.2–93.1% and 49.1–95.6% under ambient and elevated CO_2 respectively. The experiment was carried out for two consecutive years in the dry seasons (January to April) of 2014 and 2015. The total rainfall during the growing season of 2014 was 82.3 mm and during 2015 was 72 mm only, which was very less as compared to total irrigation water input which varied from 610 to 1270 mm over both the years.

Pure CO_2 gas and air was mixed in pressurized CO_2 and air mixing chamber (99.99% pure CO_2; Outlet CO_2 pressure 3 kg cm^{-2}) and then the CO_2 enriched air was blown (2.5 kg cm^{-2} pressure) inside the OTCs through perforated polyvinyl tubes regulated by solenoid valves. The CO_2 data logging, sampling and injection through solenoid valves were performed by a PC through automatic digital input and output components and a customized microcontroller providing real time control (Roy et al., 2012, 2015; Bhattacharyya et al., 2013, 2014, 2016). The ECO_2 concentration inside the OTCs was continuously monitored by a CO_2 analyser and the fluctuations of CO_2 concentration within the OTCs were about ± 20 μmol mol^{-1}. During the entire crop growth period, the ECO_2 concentration was maintained during the day time (8 AM to 5.30 PM). The plants would respond to ECO_2 only during day time as CO_2 is mainly used by the plants in the process of photosynthesis, for which light is an essential requirement. During night time plant will not respond to ECO_2 due to absence of photosynthesis (Abebe et al., 2016).