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Combined effect of elevated CO_2 and temperature on dry matter production, net assimilation rate, C and N allocations in tropical rice (*Oryza sativa* L.)

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ABSTRACT

A field experiment was carried out for 3 years to observe the effects of ambient CO_2 (390 μmol mol^{-1} in open field (UC) as well as control chamber (CC)), elevated CO_2 (EC) (550 μmol mol^{-1}) and elevated CO_2 (550 μmol mol^{-1}) + elevated temperature (+2 °C over control chamber) (ECT) on dry matter (DM) production, carbon (C) and nitrogen (N) concentrations in plant parts and its allocation in a tropical rice cultivar (cv. *Naveen*, photoperiod non-sensitive) under open top chambers (OTCs). Highest increase (84.5%) in DM accumulation in the above ground portion was noticed under ECT than that under CC at the panicle initiation stage over three *kharif* cropping season. Root biomass, leaf area index (LAI) and net C assimilation rates (NAR) increased significantly under EC than CC by 28, 19 and 40%, respectively. The grain yield was also significantly higher under EC compared to CC (22.6%), although the higher temperature in ECT reduced the yield advantage by 3% than EC over 3 years. The C concentrations in stem, leaves and roots were highest at the heading stage and increased significantly by 5, 4.8 and 4.9% in stem, leaves and roots, respectively under EC over CC. The net C yield increased both under EC and ECT by 23.3 and 24.2% than CC over the period of 3 years, respectively. The order of C and N allocations in different plant parts was panicles > root > stem > leaves. The N use efficiency for grain increased significantly under EC.

1. Introduction

The atmospheric concentration of carbon dioxide has increased by 24% to a current level of 394 μmol mol^{-1} (http://weatherdem.wordpress.com) since 1958 (NOAA, 2007), with projected increases to 700–800 μmol mol^{-1} CO_2 by the end of 21st century (IPCC, 2007). Ongoing and projected changes in atmospheric carbon dioxide and other greenhouse gases may result in uncertain climatic changes related to temperature, precipitation, etc., with negative consequences for global food supply (Lobell and Field, 2007). Global mean surface air temperature has increased about 0.74 °C for the past 100 years, and is anticipated to rise by about 1.1–6.4 °C by the end of this century (IPCC, 2007). This means that the climate may become warmer with a decreasing trend in the diurnal temperature range (IPCC, 2007). The predicted 2.0 °C increase in air temperature by the end of 2050 (IPCC, 2007) might lead to a 20–40% decrease in cereal yields, mostly in Asia and Africa (Lele, 2010). Meanwhile, an average annual increase in grain production of 44 million metric tons is required to meet the food demands of the world by 2050 (Tester and Langridge, 2010). Although most of the quantitative evaluations of warming impacts were based on crop model projections (Sheehy et al., 2006) and historical data analyses (You et al., 2009), great uncertainties remain due to the unclear understanding of the actual crop response (Tubiello et al., 2007). The production of rice is markedly affected by both atmospheric concentration of CO_2 ([CO_2]) and air temperature (Cheng et al., 2010). To predict the effects of global warming, several studies have been conducted during the past decades to analyze the effects of EC on rice growth and yield in controlled-environment chambers and field experiments (Sasaki et al., 2007; Ma et al., 2007). Those results showed that EC would increase rice yield, as rice is a C3 species and generally responds favorably to increased [CO_2] by increasing its carbon assimilation rates. On the contrary, studies have shown that high air temperatures can reduce grain yield even under CO_2 enrichment (Horie et al., 2000) owing to problems with the pollination process that lead to increased spikelet sterility (Matsui et al., 1997). Yield and nutrient (such as C and N) accumulation in rice are virtually dependent on the process of DM production. Nakagawa and Horie (2000) demonstrated that EC and elevated air temperature greatly increased DM accumulation of rice. Carbon and N are critical to many aspects of plant physiological functioning and microbial metabolism and can have a significant effect on the growth responses of many crops, including rice (Kimball et al., 2002). The effects of rising CO_2 levels on the coupled cycling of C and N will have critical impact on ecosystem function today and in the future (Luo et al., 2008). On the other hand, rising temperatures are likely to increase plant respiration and soil N mineralization and

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modulate the effects of EC (Pendall et al., 2004). Hence, there is a need to determine the effect of elevated CO_2 on C and N allocations in different vegetative parts over the entire growth period of rice. Research data on the response of rice on C and N accumulation and its partitioning in different parts of plant under EC at high temperatures (i.e. >30 °C) in humid tropical environments is limited (De Costa et al., 2003a,b; Weerakoon et al., 2005). It is hypothesized that the allocations of C and N would be altered under EC as well as ECT in accordance to the DM accumulation and C and N concentrations. The main objective of the present study was (i) to determine the yield, DM accumulation, NAR and C and N use efficiency in rice under EC and ECT, and (ii) to determine the C and N concentrations and their allocations in different parts of the rice crop.

2. Materials and methods

2.1. Experimental site

The study site is situated at the experimental farm of the Central Rice Research Institute, Cuttack (20°25′N, 85°55′E; 24 m above mean sea level), in the eastern part of India. The climate of this area is characterized by tropical climate, with short winter and lengthy hot summer period and heavy cyclonic rainfall during monsoon. The mean annual precipitation is around 1500 mm of which 75–80% is received between June and September. The soil is an Aeric Endoaquept with sandy clay loam texture (25.9% clay, 21.6% silt, 52.5% sand), bulk density 1.40 $Mg\,m^{-3}$, percolation rate <10 $mm\,d^{-1}$, pH (H_2O) 6.36, cation exchange capacity 15.3 c mol (p+) kg^{-1}, electrical conductivity 0.49 $dS\,m^{-1}$, total C 0.77% and total N 0.08%.

2.2. Experimental design

The CO_2 enrichment experiment was conducted in circular shaped, UV shielded open-top chambers (OTCs; diameter 4 m and height 3 m) (M/S Neogenesis Engineering, Thane, Maharashtra, India). The chambers (replicated twice in randomized block design (RBD) in the field) were lined with transparent multilayered polycarbonate sheets, constructed and placed on the flooded rice field with cement grouting. The rice plants were cultivated in the field inside the OTCs throughout the crop growing season. The treatments included (i) in open field (i.e. unchambered control) UC (390 ± 10 $\mu mol\,mol^{-1}$ CO_2), (ii) CC (390 ± 10 $\mu mol\,mol^{-1}$ CO_2), (ii) EC (550 ± 30 $\mu mol\,mol^{-1}$ CO_2), (iii) ECT (550 ± 30 $\mu mol\,mol^{-1}$ CO_2 associated with 2 °C higher air temperature compared to control chamber). For all 3 years of the study [CO_2] treatments were maintained 24 $h\,d^{-1}$ throughout the crop growing season until physiological maturity. The mixing of CO_2 (99.99% pure CO_2; Outlet CO_2 pressure 3 $kg\,cm^{-2}$ from manifold system connected with CO_2 gas cylinder) and air were done in pressurized CO_2 and air mixing chamber with air filter regulator which was attached to the high capacity air compressor (outlet air pressure 7 $kg\,cm^{-2}$). The CO_2 enriched air was pushed (2.5 $kg\,cm^{-2}$ pressure) inside the chambers 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 automated digital input and output module (DOIP) and customized microcontroller based system (OTMATIC; M/s Magnetic Brains, Mumbai, Maharashtra, India) on real time basis. The CO_2 concentration and temperature in UC were monitored by portable photosynthetic system (LICOR, model no. LI-6400XT). Gas samples were withdrawn from all elevated and ambient CO_2 chambers at 3 min intervals at canopy height and adjustments of desired CO_2 concentration were made in the chambers. Average carbon dioxide concentrations [CO_2] (determined by CO_2 analyzer (Model ZFP9AB41, M/S Fuji Electric, Japan), were 380 ± 12, 394 ± 15 and 398 ± 9 $\mu mol\,mol^{-1}$ (mean ± SD between replicates) in daytime and 470 ± 21, 460 ± 10 and 480 ± 25 $\mu mol\,mol^{-1}$ (mean ± SD between replicates) in night times under CC treatment in 2009, 2010 and 2011, respectively. Micro-meteorological conditions of photosynthetic photon flux indicated that the chamber transmitted 84–88% of all incoming light. The light intensity inside and outside the OTCs was measured frequently using a quantum radiometer. The average daytime temperature in UC, CC, EC and ECT was 31.3 ± 2.1, 31.8 ± 2.0, 32.9 ± 1.6 and 33.7 ± 1.7 over the period of 2009–2011, respectively. The average daytime increase in temperature under EC was 1.0, 1.2 and 1.4 °C above the ambient temperature (in comparison to CC) for 2009, 2010 and 2011, respectively. The relative humidity (RH) varied in the range of 65.5–95.4%, 68.5–98.2% and 61.1–91.4% under CC, EC and ECT over the period of 2009–2011. The elevated temperature was maintained by putting Infrared lamps (IR) inside the OTC and was controlled by the automatically calibrated temperature sensors. The IR lamps transfer heat to the soil and air above the surface without direct contact of a heating element on the soil (Harte et al., 1995). In this study, the temperature of air inside the ECT chambers get warmed by the IR lamps (M/s AEC Heaters Pvt. Ltd., Mumbai, India) indirectly through transfer of heat from water surface, soil and above ground portion of rice plants. There were two IR lamps (each of 1000 W output) in each ECT chamber hanged 2.0 m above the soil surface. The operating wavelengths of the infrared heaters were above 1000 nm. The lamps were equipped with ceramic core coated with incoloy, a metal alloy effective in high temperature applications ensuring a consistent infrared wavelength. The on/off action of infrared lamps was controlled by power semi-conductor controllers operated by the program logic control (PLC) (OTMATIC; M/s Magnetic Brains, Mumbai, Maharashtra, India). Air temperature and relative humidity was monitored continuously at every 5 min interval in each OTC by temperature–humidity calibrated sensors (IMD, Pune, Maharashtra, India).

2.3. Crop cultivation

The field experiment was laid out for 3 years under intensive rice-rice cropping pattern. The wet season or *kharif* (July–October) rice was grown under irrigated condition. The field was ploughed thoroughly and flooded 2–3 days before transplanting for puddling and leveling. Seedlings were raised in seed trays kept under the respective treatments. Over the three *kharif* cropping season the sowing of the seedlings were done in the month of June (on 25th, 20th, 18th June in the year 2009, 2010 and 2011, respectively) and transplanting was done in the month of July (on 18th, 15th, 13th July in the year 2009, 2010 and 2011, respectively). The harvest of the crop was accomplished on 26th, 20th and 21st October of the year 2009, 2010 and 2011 respectively. The important growth stages included maximum tillering (30–35 days after transplanting (DAT)), panicle initiation (45–48 DAT), heading (52–56 DAT), mid-ripening (71–74 DAT) and maturity (83–88 DAT) under the various treatments of the study. Rice plants (cv. *Naveen*, photoperiod non-sensitive) were transplanted at a spacing of 15 cm × 15 cm (i.e. 45 plants in 1 m^2) with one seedling per hill. All the experimental plots received the same doses of nitrogen, phosphorous and potassium. The N was applied in the form of urea at the rate of 100 $kg\,N\,ha^{-1}$ in 3 split doses, i.e. 50% basal application (at the time of rice transplanting), 25% application in maximum tillering stage and 25% in panicle initiation stage irrespective of the treatments. Phosphorous and potassium were applied as basal in the form of single super phosphate and muriate of potash at the rate of 40 $kg\,P\,ha^{-1}$ and 40 $kg\,K\,ha^{-1}$, respectively. All the field plots remained continuously flooded to a water depth of 8 ± 5 cm during