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Application of additional dose of N could sustain rice yield and maintain plant nitrogen under elevated ozone (O_3) and carbon dioxide (CO_2) condition

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Introduction: Global food security is challenged by the increasing levels of air pollutants like ozone (O_3) through their impacts on crop productivity. The present study was conducted to quantify the interactive effect of elevated ozone (O_3) and carbon dioxide (CO_2), on different rice varieties in northern India.

Methods: An experiment was conducted in Genetic H field, Environment science, IARI for two consecutive years (2020 and 2021) during the *kharif* season, to quantify the impact of elevated O_3 and CO_2 interaction on productivity, and plant N in three rice varieties (Pusa basmati 1121, Nagina 22, IR64 Drt1) under different nitrogen (N) management practices. Rice crop was grown in Free Air Ozone-Carbon dioxide Enrichment rings (FAOCE) rings with two levels of O_3 (elevated 60 $\pm$10ppb and ambient) and two levels of CO_2 (elevated, 550$\pm$25 ppm and ambient) concentration and their interaction with two N fertilizer treatments i.e., 100% RDN (recommended dose of N) and 125% RDN.

Results and discussion: Elevated O_3 significantly decreased physiological parameters like photosynthesis rate, stomatal conductance and transpiration rate of the crop. Grain yield reduced by 7.2-7.5%, in Pusa Basmati 1121 and from 6.9-9% in IR64 Drt1 varieties in elevated O_3 treatment as compared to ambient treatment. Yield reduction in Nagina 22 variety was not significant in elevated O_3 treatment. Elevated CO_2 concentration of 550 ppm was able to fully compensate the yield loss in Nagina 22 variety and partially compensate (3.9-8.0%) in Pusa Basmati 1121 and IR64 Drt1 varieties. Grain N concentration in rice varieties decreased by 10.8-14.7% during first year and by 7.8-20.6% during second year in elevated O_3 plus CO_2 interaction treatment than ambient. Grain N uptake also decreased (13.2-17.1% in first year and 4.5-22.8% in second year) in elevated O_3 plus CO_2 interaction treatment as compared to ambient. Application of additional 25% of recommended dose of N improved grain N concentration, grain N uptake as well as available N of soil as compared to 100% RDN treatment in elevated O_3 plus CO_2 interaction treatment. Additional 25% N dose could help in sustaining rice productivity and quality under elevated O_3 and CO_2 condition.

KEYWORDS

elevated O_3, elevated CO_2, N management, plant nitrogen, rice variety

Introduction

Air pollution is only one of several environmental issues that threaten food production. Tropospheric ozone (O_3) is one of the major air pollutants harmful to plants (Feng et al., 2015). The O_3 pollution is expected to worsen in the future due to a warmer climate, depending on the location, and increased anthropogenic emissions of O_3 precursors.

Following the Industrial Revolution, the percentage of ground-level O_3 has been steadily rising, reaching 35–40 ppb globally. In the 21st century, it may continue to rise more rapidly in developing countries with fast-growing economies (Proietti et al., 2016). The tropospheric O_3 level might exceed 70 ppb by 2050, according to the Environmental Protection Agency, if worldwide emissions of O_3 precursors continue at their current rate (Pfister et al., 2014). Tropospheric O_3 concentrations are increasing at a higher rate in tropical regions due to favorable conditions for O_3 formation (Agrawal et al., 2003; Tiwari et al., 2008). Following the mid-1990s, the decadal increase in tropospheric O_3 levels has been 2–14% in the tropics, 2–7% in northern mid-latitude areas, and 8–14% in the South Asian region (IPCC, 2021). Tropospheric O_3 is created as a secondary pollutant in the atmosphere through photochemical interactions between volatile organic compounds (VOCs) and nitrogen oxides (NOx) in the presence of sunlight (Lefohn et al., 2017). Due to increased economic growth accompanied by higher NOx and VOC emissions, tropospheric O_3 levels are rising and are expected to continue to do so across the Asian region, leading to more crop losses (Ashmore, 2005). The O_3 concentration ranged from 45 to 65 ppb across the Indian region (David and Nair, 2013; Deb Roy et al., 2009). In most regions of the world, ozone is now the most significant air pollutant that has a detrimental effect on the growth and productivity of crops. Tropospheric O_3 is also a greenhouse gas (GHG) and contributes to climate change (Feng et al., 2019). Exposure to O_3 leads to stomatal closure, which limits carbon dioxide (CO_2) and water uptake by plants, further compromising photosynthetic efficiency and causing reduced growth and decreased grain filling in crop plants (Feng and Kobayashi, 2009). Several studies have quantified the impact of O_3 on crop development and yield (Ainsworth, 2008; Mills et al., 2018; Tai et al., 2014; Yadav et al., 2021). There are reports of reduced photosynthesis rates, leaf senescence, and changes in assimilate partitioning in plants due to exposure to elevated levels of O_3 (Mina et al., 2016; Tomer et al., 2015). Increased concentrations of surface O_3 diminish carbon storage in vegetation, leading to reduced growth and yield of crops (Tai et al., 2014). On the other hand, elevated atmospheric CO_2 concentrations lead to the accumulation of carbon, thereby increasing crop growth and also reducing plant nitrogen (N) and protein content (Abebe et al., 2016; Chakrabarti et al., 2020; Raj et al., 2019). The global average concentration of CO_2 has increased from 280 ppm to 409.7 ppm (NOAA, ESRI, 2019). An increase in atmospheric CO_2 concentrations improves the growth and productivity of crop plants (Bhatia et al., 2012; Singh et al., 2013; Deryng et al., 2016).

The world's most important food crop, rice, is vulnerable to a variety of contaminants, especially air pollutants such as tropospheric O_3. Global food security is likely to suffer if the productivity of rice declines. Elevated tropospheric O_3 levels cause stress to rice plants during both the vegetative and reproductive stages, affecting their physiology, yield, and grain quality. According to Xia et al. (2021), major food crops, such as rice, wheat, and maize, are less tolerant to elevated O_3 than trees, such as spruce, silver fir, and pine. Elevated O_3 levels can alter physiological processes in crop plants, leading to changes in crop morphology and reduced crop growth (Bhatia et al., 2013).

Some reports elevated O_3 levels reduced yield by 11.4–12.3% compared to ambient levels in rice crops (Bhatia et al., 2011). Pandey et al. (2018) observed that grain yield and grain N content in wheat decreased under elevated O_3 concentrations. Along with reduced plant growth and productivity, higher O_3 levels also affect grain quality in crops as it is a strong oxidant and reduces important physiological processes in plants (Avnery et al., 2011; Broberg et al., 2015). Some researchers have reported that protein content in crops gets negatively affected by elevated O_3, but to a lesser extent than grain yield (Broberg et al., 2015; Grünhage et al., 2012). The interactive effect of elevated O_3 and CO_2 on crop growth, yield, and plant nutrient content will differ from the individual effect of O_3. Phothi et al. (2016) reported that elevated CO_2 levels would mitigate the negative impact of elevated tropospheric O_3 in rice crops. A simultaneous increase in both O_3 and CO_2 concentrations could nullify the negative effects of elevated O_3 on the ecosystem (Bhatia et al., 2012). Therefore, the negative effects of elevated tropospheric O_3 would be overestimated if the impact of elevated CO_2 concentrations is not considered (Xia et al., 2021).

Crop productivity is affected by the availability of N supplied to plants through various sources, including inorganic fertilizers. The interaction between O_3 and CO_2 will also affect the nutrient levels in crops (Phothi et al., 2016). As crop growth is reduced under elevated O_3 conditions (Pleijel et al., 2014), the demand and uptake of nutrients will also get altered under such situations, thereby reducing total nutrient content in plants. A study comprising data analysis of peer-reviewed literature depicted that the translocation of nitrogen from straw and leaves to grain in wheat crops was negatively affected by O_3. As N fertilizer use efficiency is reduced under elevated O_3 conditions, the risk of N losses from agroecosystems increases (Broberg et al., 2017). Elevated O_3 also affects soil microbial function and N transformation in the soil (Chen et al., 2015; Wu et al., 2016), which could, in turn, affect nutrient availability and uptake in plants. As crop productivity is often limited by nitrogen, N management becomes very crucial, especially under changing climatic conditions (Bhatia et al., 2010). A study by Singh et al. (2009) showed that the application of 1.5 times of recommended NPK can help ameliorate the negative effects of elevated tropospheric O_3 in mustard crops.

Estimating the effects of crop loss caused by tropospheric O_3 is crucial for nations, such as India, that are experiencing rapid urbanization and population growth. A few studies have investigated the interactive effects of elevated O_3 and CO_2 on crop plants. However, studies on elevated O_3 and CO_2 interactions with rice productivity and plant N are very limited. In addition, most studies were conducted earlier using open-top chambers (OTCs). It is imperative to conduct studies on the interaction between elevated levels of O_3 and CO_2 in open-field conditions, as such research is rarely reported. There is a need for a better understanding of cultivar-specific responses to elevated O_3 and CO_2 interactions to identify suitable adaptation options in rice under ozone stress conditions. In addition, N management strategies need to be formulated to sustain crop productivity and quality under elevated O_3 and CO_2 conditions. The hypothesis is that elevated O_3 and CO_2 can negatively affect rice productivity and quality. An additional N dose may counteract the harmful effects by improving growth, yield, and plant N uptake under elevated O_3 and CO_2 conditions. Therefore, the following study was conducted using a free air ozone and carbon dioxide enrichment (FAOCE) facility under open-field conditions (1) to quantify the yield and N uptake in rice varieties under the interaction of elevated O_3 and CO_2 and (2) to investigate the effect of an increased N dose on the yield and plant N in rice under elevated O_3 and CO_2 conditions.

Materials and methods

Experimental site

A field experiment was conducted during the *kharif* season (July–October) for two consecutive years, i.e., 2020 and 2021, inside free air O_3 and CO_2 enrichment (FAOCE) rings located at the experimental farm of the-Indian Agricultural Research Institute (ICAR), New Delhi (28°35'N and 77°12′E) India. The mean temperatures during the cropping season were 29.5°C in the first and 29.1°C in the second year of the study. Three different rice varieties, Pusa Basmati 1121, Nagina 22, and IR64 Drt1, were grown in crates inside the free air ozone and carbon dioxide enrichment (FAOCE) facility. Pusa Basmati 1509 is a popular basmati variety of rice in the northwestern Indo-Gangetic Plain (IGP). It is known for its long, slender grains and distinct aroma. IR64 DRT1 is a high-yielding, drought-tolerant rice variety that is resistant to major pests and diseases and can be grown in different agro-climatic conditions. Nagina 22 is a short-duration rice variety adaptable to various abiotic stresses and also resistant to pests and diseases. The rice varieties were grown under ambient and elevated (60 ppb) O_3 levels, as well as ambient and elevated (550 ± 25 ppm) CO_2 concentrations. The ambient CO_2 concentration ranged from 398 to 421 ppm and from 404 to 420 ppm in 2020 and 2021, respectively. The elevated CO_2 concentration ranged from 518 to 570 ppm and from 526 to 575 ppm in the FAOCE rings in 2020 and 2021, respectively. The 5 m diameter FAOCE rings were effective in exposing the crops to elevated O_3 and CO_2 under natural field conditions. Air mixed with CO_2 was supplied at the canopy level through perforated pipes with laser-drilled holes (0.3 mm in diameter) inside the ring from commercial-grade compressed 30 kg pure CO_2 gas cylinders. The release of CO_2 inside the rings was controlled by the opening and closing of the solenoid valves depending on the wind speed and direction (Yadav et al., 2021). Ozone generators were used to convert atmospheric oxygen (O_2) into O_3, which was then released inside the rings with the help of flappers through a common duct placed perpendicular to the rings (Yadav et al., 2019). Air samples were drawn from the center of the rings, and the CO_2 concentration was measured using a CO_2 analyzer (NDIR, Topak United States), while the O_3 concentration was measured using an O_3 analyzer (2B Technologies). The CO_2 and O_3 concentrations in the rings were automatically logged in the computer by microprocessors through digital input and output modules on a real-time basis. The crops were exposed to elevated CO_2 and O_3 for 7 h (10.00 am to 17.00 pm). Four rings were used for the study: (1) ambient CO_2 and O_3, (2) ambient O_3 and elevated CO_2, (3) elevated O_3 and ambient CO_2, and (4) elevated O_3 and elevated CO_2. Rice seedlings (30 days old) were transplanted into crates (42 cm × 63 cm) filled with 40 kg of soil inside the FAOCE rings during the second week of July. The crops were fertilized with two doses of N: the recommended dose of N (RDN) (120 kg ha^{-1}) and 125% of the recommended dose of N (150 kg ha^{-1}). Phosphorus (P) and potassium (K) were applied at the rate of 60 kg ha^{-1}. Half of the N dose and the total amount of P and K were applied at the time of transplanting. The remaining half of the N dose was applied in two equal splits at the maximum tillering and flowering stages of the crops. In total, there were 24 treatments, each with three replications.

Measurements of the crop growth parameters

Gas exchange parameters, such as photosynthesis rate, stomatal conductance, and transpiration rate, were measured using the Portable Photosynthesis System IRGA (LI-6400XT, LiCOR, United States) at the maximum tillering stage of the crops. The observations were recorded on physiologically active, fully expanded leaves exposed to the sun between 9:00 AM to 11:00 AM. The flow rate of input air was set at 300 μmol s^{-1}, and photosynthetically active radiation (PAR) was set at 1,000 μmol m^{-2} s^{-1}. The reference CO_2 concentration was maintained at 410 ppm. Ten readings were recorded for each observation in each treatment. The number of tillers per hill was also counted for each treatment. The plant samples were harvested at maturity and air-dried, and the weights of the grain and straw were recorded. The number of grains per panicle was counted after harvesting the crops for each treatment.

Soil and plant sample collection and analysis

Soil samples were collected at the flowering stage. Available N in the soil was estimated using the Subbiah and Asija (1956) method. The soil was distilled with alkaline $KMnO_4$ (potassium permanganate) and NaOH (sodium hydroxide) solutions, and the amount of liberated NH_3 (ammonia) was estimated by titration with standard H_2SO_4 (sulphuric acid). The plant samples were collected after harvesting the crops. The rice grains were separated from the straw biomass, and the samples were dried in an oven at 65 ± 2°C for 72 h. The nitrogen concentration in the grain and straw samples was determined using the method described by Jackson (1956). The plant samples were digested using concentrated H_2SO_4 and a digestion mixture in a micro Kjeldahl digestion block. The digested samples were distilled with NaOH, and the liberated NH_3 was absorbed in H_3BO_3 (boric acid) and then titrated against standard H_2SO_4. The grain N uptake (mg plant^{-1}) was then calculated by multiplying the grain weight/plant by the grain N concentration, as described by Cowan et al. (2021).

Statistical analysis

The experiment was a factorial, completely randomized design with 24 treatments, each having three replicates. Four factorial (CO_2 level, O_3 level, variety, and N dose) analysis of variance (ANOVA) was carried out using SAS (ver. 9.3) statistical package (SAS Institute Inc., CA, United States). Tukey's honestly significant difference (HSD) test at the 5% level of significance was performed to check if the differences were statistically significant.

Results

Effect of elevated O_3 and CO_2 on the rice physiology

The photosynthesis rates varied among the different rice varieties, ranging from 23.1 to 36.1 μmol CO_2 m^{-2} s^{-1} in the first year and from 23.2 to 35.1 μmol CO_2 m^{-2} s^{-1} in the second year under the recommended N dose (Figures 1a,b). Pusa Basmati 1121 exhibited a significant decrease in the photosynthesis rates, dropping from 30.3 to 26.5 μmol CO_2 m^{-2} s^{-1} in the first year and from 31.1 to 27.9 μmol CO_2 m^{-2} s^{-1} in the second year. In the case of IR64 Drt1, the photosynthesis rate was significantly lower under the elevated O_3 levels compared to the ambient levels in the second year. Conversely, there was no notable reduction in the photosynthesis rates for the Nagina 22 variety over both years under the elevated O_3 conditions. The elevated CO_2 concentration exhibited a positive impact on the photosynthesis rates of all rice varieties. However, the interactive treatment of elevated O_3 and CO_2 still maintained the photosynthesis rates similar to those under the ambient condition. The application of additional N positively influenced the photosynthesis rates across all treatments. When 25% additional N was applied, the photosynthesis

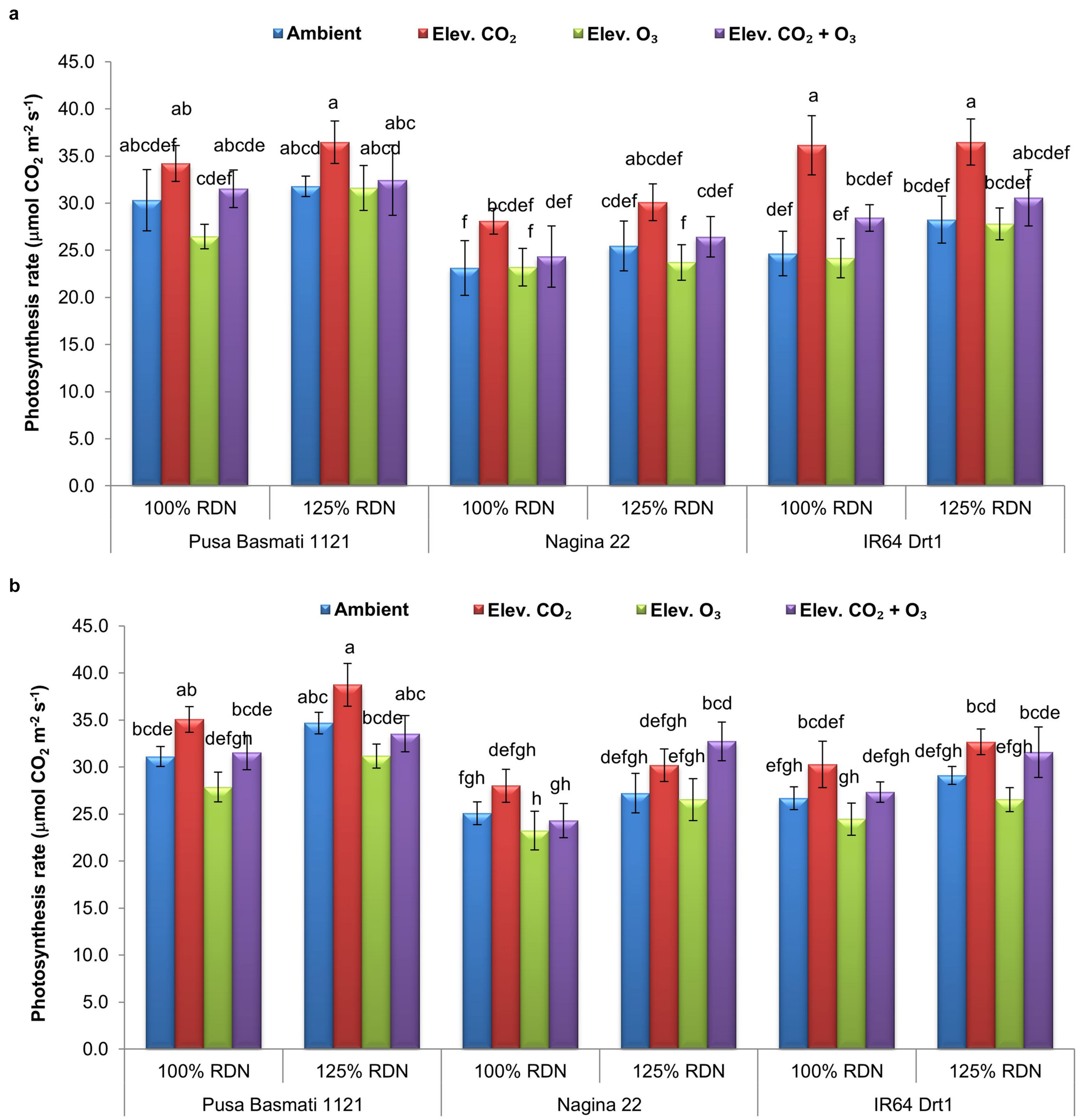

FIGURE 1
Photosynthesis rates (μmol CO_2 m^{-2} s^{-1}) in the rice varieties under the elevated O_3 and CO_2 conditions during the (a) first and (b) second year. Columns with different letters are significantly different ($p \leq 0.05$). The error bars represent the standard deviation of the data, indicating the variability around the mean.

rates in the elevated O_3 treatment became comparable to those in the ambient treatment.

Stomatal conductance in the rice varieties decreased in the presence of the elevated O_3 and elevated O_3 plus CO_2 treatments compared to the ambient treatment. In the treatments with the recommended N application, stomatal conductance ranged from 0.31 to 0.42 m mol H_2O m^{-2} s^{-1} in Pusa Basmati 1121, 0.29 to 0.31 m mol H_2O m^{-2} s^{-1} in Nagina 22, and 0.33 to 0.41 m mol H_2O m^{-2} s^{-1} in IR64 Drt1 under the ambient conditions (Figures 2a,b). However, stomatal conductance decreased in the elevated O_3 plus CO_2 treatment, ranging from 0.24 to 0.30 m mol H_2O m^{-2} s^{-1} in Pusa Basmati 1121, 0.22 to 0.24 m mol H_2O m^{-2} s^{-1} in Nagina 22, and 0.29 to 0.30 m mol H_2O m^{-2} s^{-1} in IR64 Drt1. Furthermore, the elevated O_3 and elevated O_3 plus CO_2 treatments significantly reduced transpiration rates in the Pusa Basmati 1121 and IR64 Drt1 varieties. Over the two-year study, the transpiration rates in Pusa Basmati 1121 ranged from 12.3 to 16.4 m mol H_2O m^{-2} s^{-1} in the ambient treatment, while decreasing to 9.5 from 11.9 H_2O m^{-2} s^{-1} in the elevated O_3 treatment (Figures 3a,b). Similarly, in the IR64 Drt1 variety, the transpiration rates ranged from 14.5 to 15.0 m mol H_2O m^{-2} s^{-1} in the ambient treatment, but in the elevated O_3 treatment, they ranged from 9.5 to 11.8 m mol H_2O m^{-2} s^{-1}.

Effect of elevated O_3 and CO_2 on rice yield

The elevated O_3 level significantly decreased the grain yield of the Pusa Basmati 1121 and IR64 Drt1 varieties in both years of the study. The grain yield was reduced by 7.2–7.5%, in Pusa Basmati 1121 and by 6.9–9% in IR64 Drt1 in the elevated O_3 treatment as compared to the ambient treatment (Figure 4). In the Nagina 22 variety, there was a reduction in the yield by 4.4% in the elevated O_3 treatment compared to the ambient treatment during the first year. However, in the second year, there was no reduction in the grain yield of this variety under the elevated O_3 condition. Nagina 22 is a stress-tolerant variety, which is why an increase in the O_3 levels had little to no effect on it. In the present study, the reduction in the grain yield in the elevated O_3 treatment was attributed to a lower number of panicles per hill and

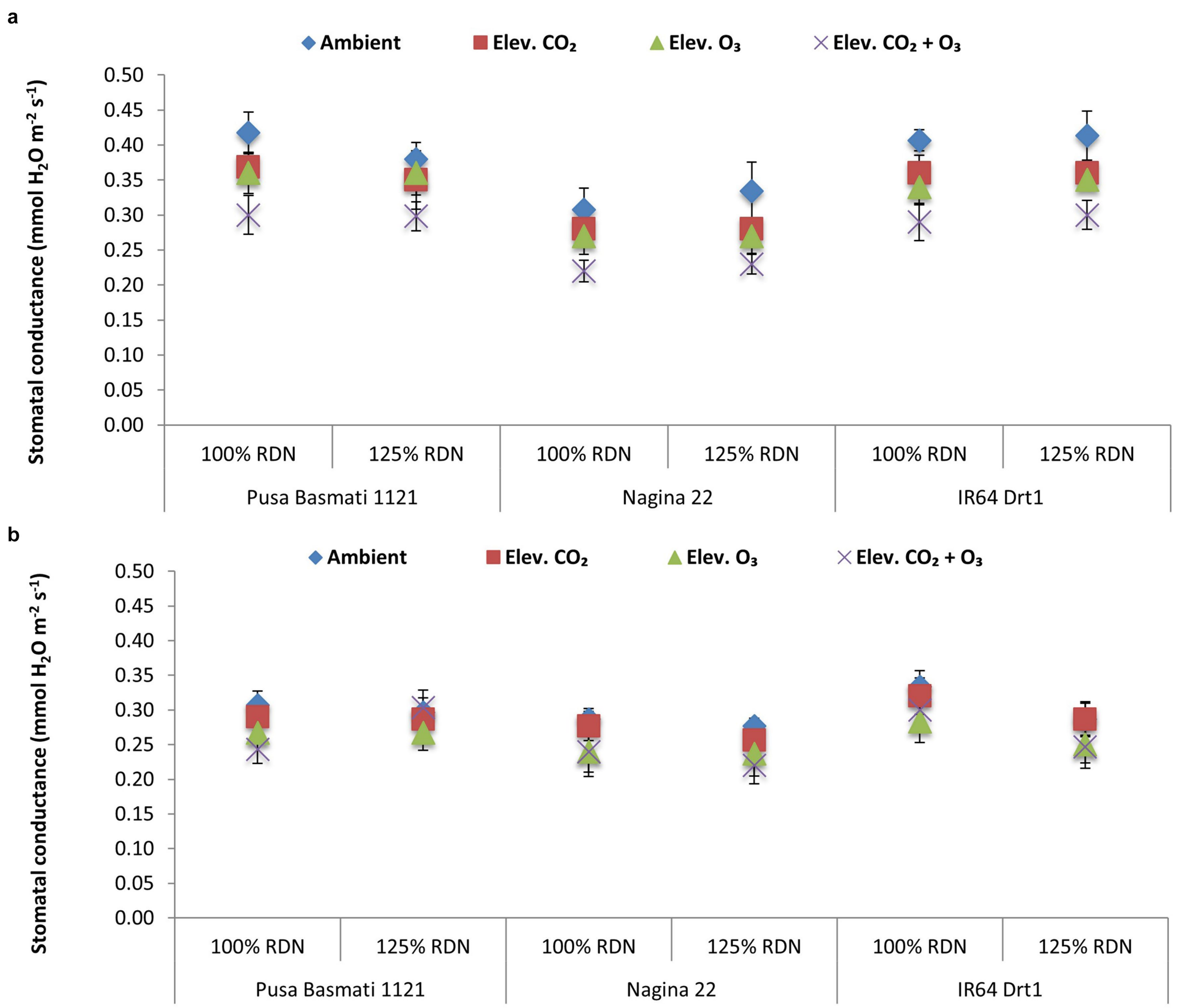

FIGURE 2
Stomatal conductance (mmol H_2O m^{-2} s^{-1}) in the rice varieties under the elevated O_3 and CO_2 conditions during the (a) first and (b) second year. The error bars represent the standard deviation of the data, indicating the variability around the mean.

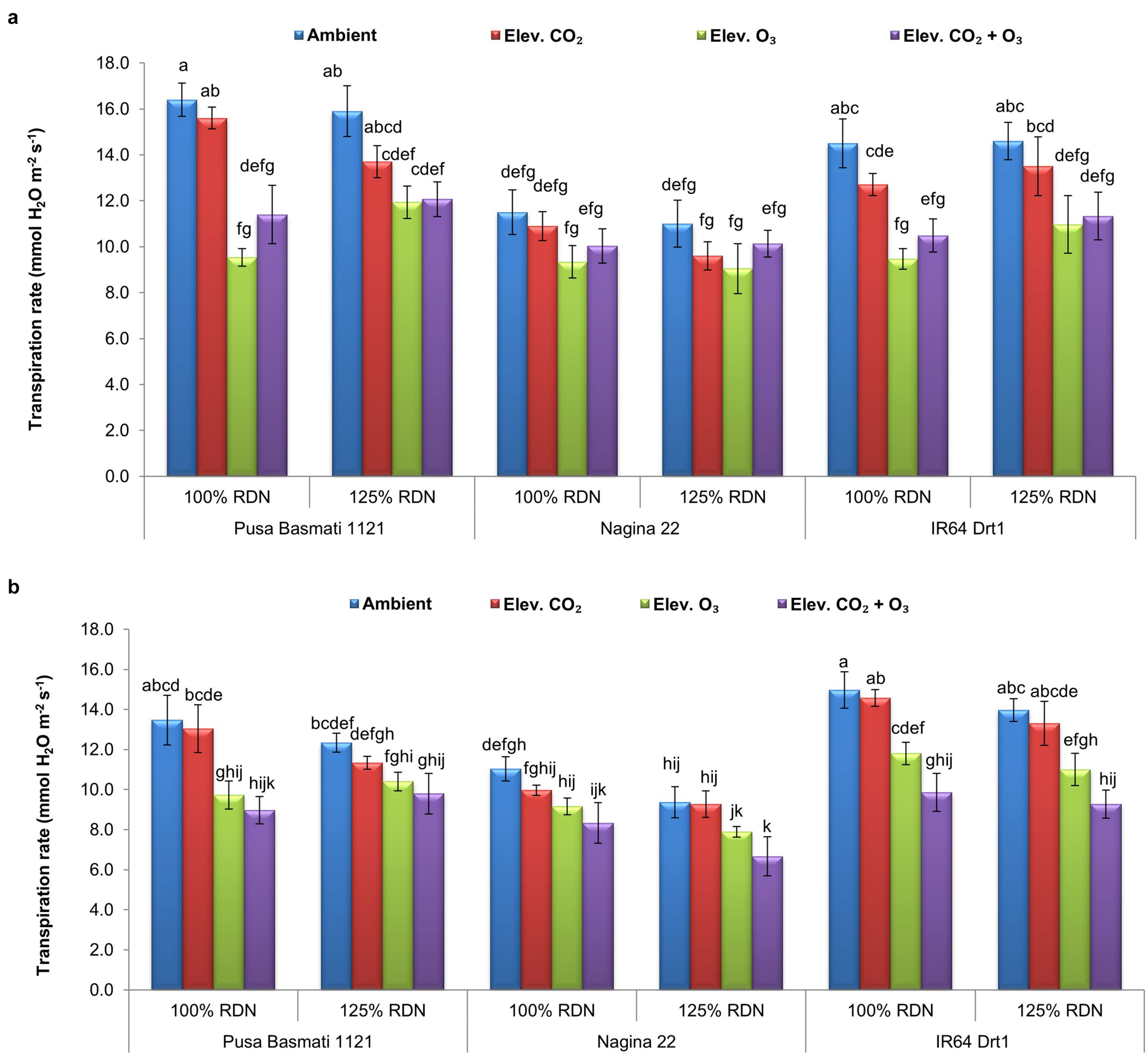

FIGURE 3
Transpiration rates (mmol H_2Om^{-2} s^{-1}) in the rice varieties under the elevated O_3 and CO_2 conditions during the (a) first and (b) second year. Columns with different letters are significantly different ($p \leq 0.05$). The error bars represent the standard deviation of the data, indicating the variability around the mean.

fewer grains per panicle under the elevated O_3 condition. Under the ambient condition, the number of grains per panicle ranged from 101 to 111 among the different rice varieties, while in the elevated O_3 treatment, the number of grains per panicle ranged from 95 to 101 (Table 1). The number of panicles per hill also decreased in the elevated O_3 treatment compared to the ambient treatment. In the ambient treatment, the number of panicles per hill ranged from 14 to 17, while in the elevated O_3 treatment, it decreased from 15 to 13.

In the elevated O_3 plus elevated CO_2 treatment, the grain yield was 2.9–3.4% lower than in the ambient treatment for the Pusa Basmati 1121 variety. This shows that the increased CO_2 concentration of 550 ppm was able to compensate for 3.9–4.6% yield loss in the Pusa Basmati 1121 variety. In the IR64 Drt1 variety, the grain yield in the elevated O_3 plus elevated CO_2 treatment was 3.4% lower than in the ambient during the first year of the study. However, during the second year, the yield was 1.1% higher than in the ambient treatment for this variety. The Nagina 22 variety recorded higher yields in the elevated O_3 plus elevated CO_2 treatment compared to the ambient treatment in both years. The application of a higher N dose also helped in preventing the yield loss in the rice varieties under the elevated O_3 concentration. In the treatment with elevated O_3 plus CO_2, along with 125% of the RDN, the grain yield of the Pusa Basmati 1121 variety increased by 11–13% compared to the ambient treatment (Figure 4). Similarly, in the IR64 Drt1 variety, the yield increased by 9–10%, and in the Nagina 22 variety, it increased by 6–7% in this treatment.

The grain number per panicle also increased in the elevated CO_2 plus elevated O_3 treatment compared to that in the elevated O_3 treatment. The elevated CO_2 level increased the photosynthesis rates of the crops, which led to greater biomass accumulation and subsequently more grains, resulting in higher crop yields. The application of a higher dose of N also increased the grain number in all three rice varieties, which led to higher crop yields. In the elevated

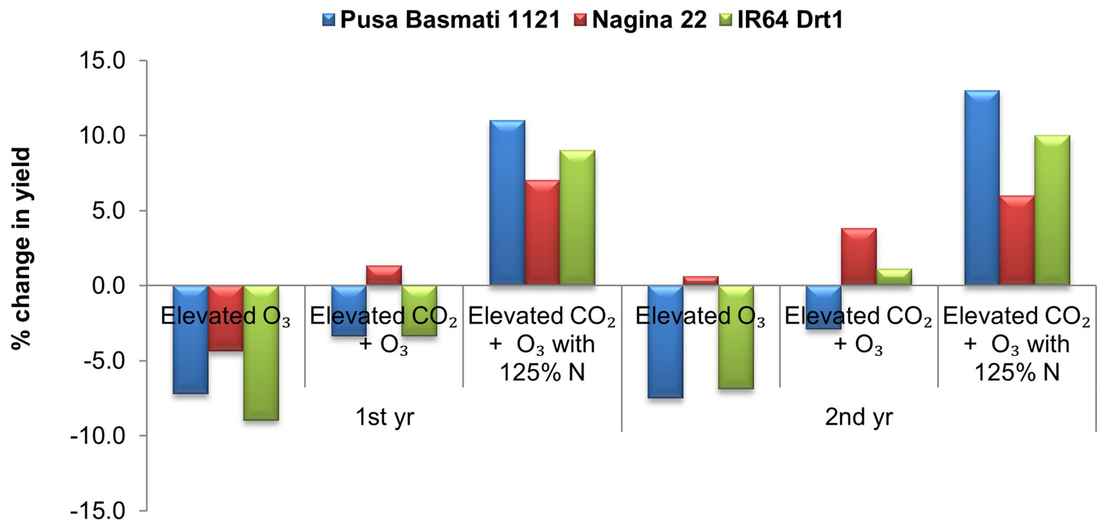

FIGURE 4
Percent change in the yield in the rice varieties under the elevated O_3 and CO_2 conditions.

TABLE 1 Effect of the elevated CO_2, O_3 and N treatments on the yield parameters of rice.

Variety	O_3	CO_2	Panicles hill^{-1}		Panicles hill^{-1}		Grains panicle^{-1}		Grains panicle^{-1}	
			First year		Second year		First year		Second year	
			100% RDN	125% RDN	100% RDN	125% RDN	100% RDN	125% RDN	100% RDN	125% RDN
PB1121	Ambient	Ambient	16.4 ± 1.8^{def}	20.2 ± 0.2^{abcd}	16.4 ± 0.5^{cdef}	18.3 ± 0.7^{abcd}	111.4 ± 3.8^{abcde}	120.4 ± 2.9^{ab}	104.9 ± 3.1^{bcd}	116.1 ± 4.5^{abc}
		Elevated	20.2 ± 25.4^{abcd}	23.3 ± 0.6^{a}	18.0 ± 1.2^{cde}	22.0 ± 0.9^{ab}	115.7 ± 6.1^{abcd}	124.9 ± 4.0^{a}	112.2 ± 3.6^{abcd}	119.3 ± 2.9^{ab}
	Elevated	Ambient	14.1 ± 1.5^{f}	18.5 ± 0.9^{abcd}	14.0 ± 1.1^{efg}	17.2 ± 1.6^{cde}	96.5 ± 3.9^{e}	105.5 ± 3.4^{bcde}	94.9 ± 3.1^{f}	101.1 ± 3.0^{cde}
		Elevated	17.4 ± 0.2^{cde}	18.8 ± 0.4^{abcd}	16.0 ± 0.8^{defg}	18.5 ± 0.8^{abcd}	106.8 ± 4.8^{bcde}	113.9 ± 6.6^{abcd}	98.9 ± 1.9^{def}	106.2 ± 1.7^{bcd}
Nagina 22	Ambient	Ambient	14.9 ± 0.5^{ef}	18.5 ± 0.8^{abcd}	13.7 ± 0.7^{fg}	16.1 ± 1.1^{cdef}	106.3 ± 2.0^{bcde}	113.3 ± 3.9^{abcd}	100.7 ± 1.3^{def}	114.0 ± 2.3^{abcd}
		Elevated	17.3 ± 0.5^{cde}	21.8 ± 0.8^{abc}	16.5 ± 0.4^{cdef}	19.2 ± 2.1^{abc}	114.9 ± 6.0^{abcd}	117.6 ± 4.2^{abc}	109.8 ± 3.3^{abcde}	116.5 ± 0.9^{abc}
	Elevated	Ambient	14.4 ± 0.6^{f}	17.7 ± 0.9^{cde}	12.5 ± 0.8^{g}	15.1 ± 1.3^{defg}	97.0 ± 1.2^{e}	104.1 ± 4.2^{cde}	98.1 ± 3.6^{ef}	105.5 ± 3.1^{bcd}
		Elevated	16.4 ± 0.5^{def}	18.0 ± 1.0^{cde}	14.0 ± 0.5^{efg}	15.9 ± 1.1^{defg}	106.3 ± 2.0^{bcde}	110.8 ± 8.9^{abcde}	99.8 ± 1.5^{def}	110.8 ± 3.7^{abcde}
IR64 Drt1	Ambient	Ambient	14.9 ± 0.6^{ef}	18.7 ± 0.6^{abcde}	17.1 ± 0.6^{cdef}	19.1 ± 10^{abc}	106.8 ± 5.9^{bcde}	110.5 ± 5.4^{abcde}	106.8 ± 0.9^{bcd}	114.3 ± 4.6^{abcd}
		Elevated	19.2 ± 1.1^{abcd}	23.1 ± 1.2^{ab}	19.7 ± 0.4^{abc}	22.8 ± 0.3^{a}	108.8 ± 4.0^{abcde}	118.5 ± 2.5^{abc}	118.3 ± 1.2^{ab}	125.2 ± 5.5^{a}
	Elevated	Ambient	14.3 ± 0.7^{f}	18.1 ± 1.1^{cde}	15.4 ± 0.7^{defg}	17.5 ± 0.5^{cde}	96.1 ± 2.0^{e}	102.4 ± 3.1^{cde}	100.6 ± 1.0^{def}	107.7 ± 2.7^{bcd}
		Elevated	17.0 ± 1.2^{def}	19.5 ± 1.1^{abcd}	16.2 ± 0.1^{cdef}	19.1 ± 0.5^{abc}	100.1 ± 7.3^{de}	108.3 ± 2.5^{bcde}	105.1 ± 3.1^{bcd}	113.3 ± 3.9^{abcd}

Numbers in each column represent the mean values along with their standard deviation. Means with at least one letter in common are not statistically significant ($p \leq 0.05$).

O_3 treatment, the application of a higher N dose also helped in increasing the panicle number and grain number, thereby increasing the grain yield to a certain extent.

Effect of elevated O_3 and CO_2 on the plant N

The responses of the grain N concentration (%) in the rice varieties to the elevated CO_2 and O_3 treatments are shown in Figure 5a. In the 100% recommended N applied treatments, the grain N concentration ranged from 1.20–1.36% under the ambient condition, with a mean value of 1.30%. The grain N concentration significantly decreased in the elevated CO_2 and elevated O_3 plus CO_2 interaction treatment compared to the ambient treatment. In the elevated O_3 plus CO_2 interaction treatment, the grain N concentration ranged from 1.07–1.18%, with a mean value of 1.13%. The application of an additional 25% of N improved the grain N concentration in both years. When the additional N dose was applied, the grain N concentration ranged from 1.25–1.33% in the elevated O_3 plus CO_2 interaction treatments, with a mean value of 1.29%. The grain N concentration was higher in the Pusa Basmati 1121 and IR64 Drt1 varieties than in the Nagina 22 variety.

Elevated O_3 also reduced the grain N uptake of the rice varieties compared to the ambient treatment. In the ambient treatment, the grain N uptake ranged from 189 to 269 mg hill^{-1}, with a mean value

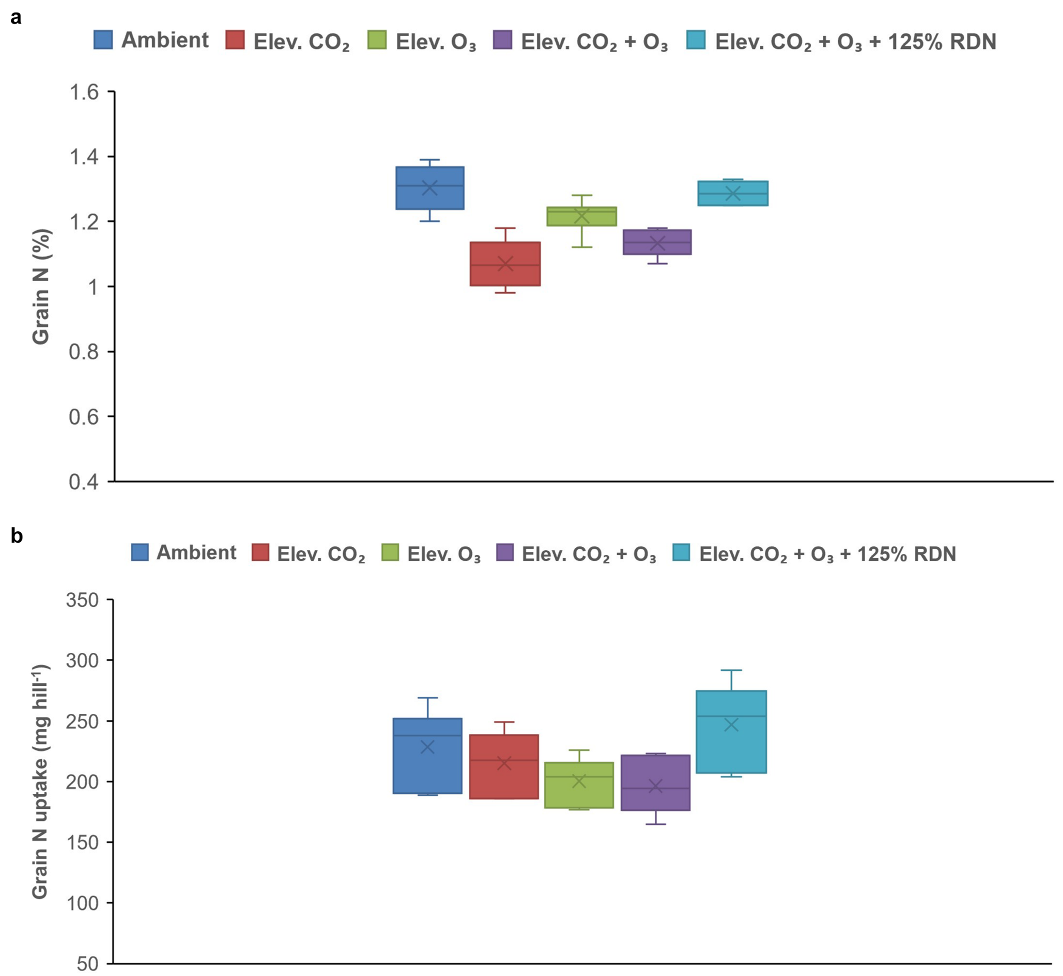

FIGURE 5
(a) Grain nitrogen concentration (%) and (b) grain N uptake (mg hill^{-1}) in the rice varieties under the elevated O_3 and CO_2 conditions. The bottom and top of the whiskers denote the first and third quartiles, respectively. The line inside the box represents the median line.

of 229 mg hill^{-1} in the treatment with the 100% RDN (Figure 5b). In the elevated O_3 plus CO_2 interaction treatment, the grain N uptake decreased and ranged from 165 to 223 mg hill^{-1}, with a mean value of 196 mg hill^{-1}. The application of a higher N dose increased the grain N uptake in the rice varieties. In the elevated O_3 plus CO_2 interaction treatment, the grain N uptake was even higher than in the ambient treatment. It ranged from 204 to 292 mg hill^{-1}, with a mean value of 247 mg hill^{-1}. The grain N uptake was greater in the Pusa Basmati 1121 and IR64 Drt1 varieties than in the Nagina 22 variety. The application of an additional 25% of N increased the grain N uptake by 30.2–40.8% in Pusa Basmati 1121, by 15.3–22.3% in Nagina 22, and by 21.7% in the IR64 Drt1 variety of the rice crops (Table 2).

Effect of elevated O_3 and CO_2 on the soil available N

In the ambient treatment, the soil available N ranged from 176.4–204.2 kg ha^{-1} in the first year and from 135.2–151.7 kg ha^{-1} in the second year among the different rice varieties with the recommended dose of the N application (Table 2). In the elevated O_3 plus CO_2 interaction treatment, the soil available N was lower than in the ambient treatment in both years of the study. The soil available N was also found to be lower in the elevated CO_2 treatment compared to the ambient treatment. The application of a higher dose of N increased the available N content of the soil. In the elevated O_3 plus CO_2 interaction treatment, the application of an additional 25% of N increased the soil available N by 5.3–14.9% in Pusa Basmati 1121, by 6.3–9.0% in Nagina 22 and by 16–16.9% in IR64 Drt1 of the rice crops.

Discussion

Tropospheric O_3 is a secondary air pollutant generated through photochemical reactions among precursors such as nitrogen oxides (NOx), volatile organic compounds (VOCs), and carbon monoxide (CO), primarily released from anthropogenic activities (Broberg et al., 2015). Several researchers have reported the substantial impact of elevated O_3 levels on crop productivity and quality (Singh et al., 2018; Yadav et al., 2019). The results from the current study showed that elevated O_3 reduced the photosynthesis rates of the Pusa Basmati 1121 and IR64 Drt1 varieties of the rice crop, while the elevated O_3 plus CO_2

TABLE 2 Effect of the elevated CO_2, O_3, and N treatments on the grain N uptake and soil available N of the rice varieties.

Variety	O_3	CO_2	Grain N uptake (mg hill^{-1})				Soil available N (kg ha^{-1})			
			First year		Second year		First year		Second year	
			100% RDN	125% RDN	100% RDN	125% RDN	100% RDN	125% RDN	100% RDN	125% RDN
PB1121	Ambient	Ambient	269.3 ± 17.9^{cde}	382.4 ± 24.1^{a}	241.5 ± 4.1^{bcdefg}	296.9 ± 4.5^{ab}	179.8 ± 9.6^{abc}	202.2 ± 18.1^{ab}	135.2 ± 4.2^{cde}	149.1 ± 8.1^{abcde}
		Elevated	249.1 ± 14.7^{cdef}	374.6 ± 21.4^{ab}	232.6 ± 18.4^{cdefgh}	279.5 ± 13.8^{abc}	147.5 ± 9.1^{c}	172.8 ± 4.8^{abc}	118.0 ± 5.7^{e}	136.5 ± 4.5^{bcde}
	Elevated	Ambient	226.4 ± 14.5^{cdef}	288.3 ± 16.2^{bcd}	196.6 ± 17.9^{fgh}	240.3 ± 7.4^{bcdefg}	172.5 ± 5.4^{abc}	194.2 ± 9.8^{abc}	129.0 ± 2.1^{cde}	139.9 ± 4.0^{bcde}
		Elevated	223.4 ± 11.1^{cdef}	292.2 ± 13.9^{abcd}	186.4 ± 16.8^{gh}	261.2 ± 18.6^{abcde}	167.1 ± 11.0^{abc}	175.6 ± 7.2^{abc}	120.2 ± 6.8^{de}	138.1 ± 7.4^{bcde}
Nagina 22	Ambient	Ambient	190.6 ± 15.0^{ef}	254.2 ± 20.1^{cdef}	188.6 ± 13.2^{gh}	233.5 ± 4.5^{cdefgh}	176.4 ± 6.7^{abc}	185.6 ± 13.2^{abc}	151.7 ± 6.9^{abc}	166.9 ± 1.9^{ab}
		Elevated	186.0 ± 18.4^{ef}	258.3 ± 20.8^{cde}	186.4 ± 24.4^{gh}	244.0 ± 16.1^{bcdefg}	169.3 ± 9.6^{abc}	162.5 ± 10.2^{bc}	129.0 ± 1.5^{cde}	140.4 ± 4.0^{abcde}
	Elevated	Ambient	179.2 ± 7.5^{ef}	203.0 ± 5.9^{def}	177.1 ± 6.1^{h}	251.9 ± 10.3^{abcdef}	170.4 ± 2.8^{abc}	162.9 ± 13.0^{bc}	137.8 ± 5.7^{bcde}	150.4 ± 10.1^{abcd}
		Elevated	165.4 ± 22.0^{f}	204.0 ± 4.6^{def}	180.1 ± 5.4^{h}	207.6 ± 7.8^{fgh}	157.8 ± 6.1^{bc}	171.8 ± 7.5^{abc}	136.7 ± 3.3^{bcde}	145.4 ± 6.3^{abcde}
IR64 Drt1	Ambient	Ambient	235.2 ± 7.7^{cdef}	300.3 ± 22.2^{abc}	245.6 ± 8.0^{bcdefg}	305.0 ± 16.2^{a}	204.2 ± 10.0^{ab}	216.7 ± 11.1^{a}	144.9 ± 4.9^{abcde}	172.6 ± 6.4^{a}
		Elevated	201.8 ± 10.7^{def}	260.2 ± 2.7^{cde}	235.3 ± 4.5^{cdefgh}	305.5 ± 18.8^{a}	147.5 ± 9.5^{c}	168.9 ± 7.7^{abc}	119.1 ± 4.9^{e}	143.7 ± 6.5^{abcde}
	Elevated	Ambient	211.3 ± 8.2^{cdef}	247.0 ± 18.7^{cdef}	212.2 ± 7.0^{defgh}	263.1 ± 10.3^{abcde}	162.5 ± 10.2^{bc}	166.8 ± 8.3^{abc}	136.4 ± 5.6^{bcde}	154.1 ± 6.8^{abc}
		Elevated	203.0 ± 7.3^{def}	270.0 ± 16.4^{cde}	221.0 ± 5.3^{cdefgh}	269.1 ± 15.7^{abcd}	161.7 ± 6.6^{bc}	188.9 ± 7.7^{abc}	134.9 ± 3.0^{cde}	157.8 ± 9.7^{abc}

Numbers in each column represent the mean values along with their standard deviation. Means with at least one letter in common are not statistically significant ($p \leq 0.05$).

treatment was able to maintain the photosynthesis rates of the crops. The elevated O_3 and elevated O_3 plus CO_2 treatments significantly reduced the stomatal conductance and transpiration rates of the Pusa Basmati 1121 and IR64 Drt1 varieties. Previous studies have also indicated that elevated O_3 could hinder photosynthetic carbon acquisition in crops (Guidi et al., 2001; Morgan et al., 2003; Singh et al., 2009; Bhatia et al., 2012). There are reports that elevated CO_2 concentrations reduce stomatal conductance and transpiration rates in rice crops (Maity et al., 2023; Zhang et al., 2022). The elevated O_3 level substantially decreased the yield of the Pusa Basmati 1121 and IR64 Drt1 varieties. In contrast, the Nagina 22 variety demonstrated comparatively less or no yield reduction. Nagina 22 is known for its stress tolerance, and the results indicate that the increase in the O_3 concentration had minimal to no effect on its yield. Such yield losses under the O_3 exposure occurred due to the reduction in photosynthesis, which reduced the supply of assimilates required for reproductive development and seed growth (Feng et al., 2010). Tatsumi et al. (2019) also reported that brown rice yield was significantly reduced under elevated O_3 concentrations. A similar decrease in grain yield with exposure to elevated O_3 concentrations was reported for wheat cultivars in north India (Daripa et al., 2016; Yadav et al., 2019). In our study, an elevated CO_2 concentration of 550 ppm was able to partially mitigate the reduction in the grain yield due to increased O_3 exposure in the Pusa Basmati 1121 and IR64 Drt1 varieties, while it fully compensated for the yield reduction in the Nagina 22 variety. Elevated CO_2 has a fertilization effect on crops, which has helped compensate for yield losses in different rice varieties. The yield loss in the Nagina 22 variety, which is stress-tolerant, was already less than the other varieties. Therefore, the reduction in the yield in Nagina 22 was fully compensated under the elevated CO_2 plus O_3 treatment. Various researchers have earlier reported the beneficial effects of increased CO_2 levels in terms of increasing yields in different crops (Dey et al., 2017; Kobayashi et al., 1999; Pramanik et al., 2018; Sanyal et al., 2023). Bhatia et al. (2021) observed that a high CO_2 concentration of 554 ppm was able to counter the harmful impacts of O_3 exposure on yield and nutrient content in chickpeas. A study conducted with rice showed that elevated CO_2 could counter yield reduction due to O_3 exposure by more than 40% (Kumar et al., 2021).

The application of a 25% higher dose of N increased the photosynthesis rates and different yield parameters, such as the number of panicles and the number of grains per panicle, in the rice crops, thereby increasing the yield to a certain extent under the elevated O_3 concentration. According to Chen et al. (2018), decreased photosynthesis in nitrogen-deficient leaves increases the yield sensitivity of crops to high O_3 concentrations. Therefore, the increased dose of N had a positive effect on the yield parameters of the rice crops even under the elevated O_3 condition. The beneficial impact of higher N doses was also reported by Raj et al. (2019), who observed that increased atmospheric CO_2 concentrations and higher N doses synergistically contributed to an increase in the panicle number, thereby improving the yield of rice crops.

The elevated O_3 plus CO_2 interaction decreased the grain N concentration and N uptake in the rice varieties compared to the ambient condition. As O_3 is a strong oxidant, it harmfully affects important physiological functions in plants, which leads to reduced quality in crops (Avnery et al., 2011). Similar findings have been reported by earlier researchers, who found that protein content in plants is negatively affected by increased O_3 (Broberg et al., 2015;

Grünhage et al., 2012). Broberg et al. (2017) reported that O_3 impairs the N translocation from straw to grain, thereby reducing the N use efficiency of crops. In addition, the applied N fertilizer is used less efficiently under elevated O_3, leading to adverse effects on grain protein content in crops. Under elevated CO_2 conditions, higher photosynthesis rates lead to greater carbon assimilation in rice, thereby reducing plant N concentrations due to the dilution effect (Kim et al., 2001). Reports indicate that protein content and N content in plants, especially cereal crops, decrease under elevated CO_2 conditions (Abebe et al., 2016; Chakrabarti et al., 2020; Raj et al., 2019).

Soil available N is also negatively affected by elevated O_3 and CO_2 treatment, which may be attributed to increased N losses from crop fields under elevated O_3 (Broberg et al., 2017). Under O_3 exposure, plant photosynthesis and grain filling duration are shortened (Gelang et al., 2000), which reduces the nutrient uptake period and increases the likelihood of greater N loss from the soil. Earlier studies (Chakrabarti et al., 2020; Maity et al., 2020) have also reported a decrease in soil available N under elevated CO_2 conditions due to increased crop growth resulting in higher N demand by the crop. As plant photosynthesis is hampered under increased O_3 concentrations, reduced photosynthates in the roots affect the root system and various soil processes (Chen et al., 2008). This may further affect soil N transformation rates (Wu et al., 2016), thereby lowering the available N status in the soil. The application of a higher N dose increased both the grain N uptake and soil available N in rice. As the crop growth was greater under the higher N doses, this generated more aboveground and belowground biomass of the crops. This might have led to increased microbial activity in the rhizosphere, leading to enhanced availability of N to the plants.

The study showed that although the negative effects of elevated O_3 on the rice yield were negated by the elevated CO_2 concentration, the adverse effect of elevated O_3 on the grain N content could not be compensated for. The response of rice to elevated CO_2 may be limited when nitrogen levels are sub-optimal. However, the decrease in plant N could be alleviated to a certain extent by applying higher doses of N (Maity et al., 2020). Our study showed that the application of the 25% RDN improved both the grain N concentration and grain N uptake, as well as soil available N, in the rice crops under the elevated O_3 and CO_2 interaction.

Conclusion

The grain yield of the rice varieties decreased under the elevated O_3 condition. An elevated CO_2 concentration of 550 ppm was able to compensate for the yield loss by 3.9–4.6% in the Pusa Basmati 1121 rice variety and by 4.6–8.0% in the IR64 Drt1 variety. Although elevated CO_2 was able to compensate for the yield loss due to elevated O_3, the N content in the rice grains was further reduced in the elevated O_3 plus CO_2 treatment. The application of an additional 25% of the recommended dose of N improved the grain N uptake by 15.3–40.8% in the different rice varieties compared to the 100% RDN in the elevated O_3 plus CO_2 interaction treatment. The study shows that nitrogen in rice grains and soil available N will decrease under elevated O_3 plus CO_2 conditions. An elevated CO_2 concentration of 550 ppm will be able to compensate for yield loss to a certain extent, but grain quality will further deteriorate in the elevated O_3 plus CO_2 treatment. The application of an additional 25% of the recommended dose of N could help in sustaining rice yield and also maintaining plant and soil N under elevated O_3 and CO_2 conditions in the future. However, the response of rice varieties to elevated O_3 and CO_2 might vary with different climate types. Therefore, the findings of the study could be further improved by testing different N fertilizer formulations to suggest the best N management options for the sustaining productivity and quality of rice under elevated O_3 and CO_2 conditions.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

BC: Formal analysis, Investigation, Project administration, Visualization, Writing – original draft, Writing – review & editing. SS: Funding acquisition, Project administration, Writing – review & editing. AM: Funding acquisition, Project administration, Writing – review & editing. SK: Investigation, Writing – original draft. VK: Methodology, Writing – original draft. SB: Conceptualization, Writing – review & editing. AB: Conceptualization, Formal analysis, Writing – review & editing, Project administration, Supervision.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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