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Research paper

Co-elevation of atmospheric CO_2 and temperature affect instantaneous and intrinsic water use efficiency of rice varieties

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ABSTRACT

Greenhouse gas (GHG) emissions from anthropogenic activities are the most significant drivers of climate change, which has both direct and indirect effects on crop production. The study was conducted during the *kharif* season for two years inside the Open Top Chamber (OTC) at the Genetic-H field of ICAR-Indian Agriculture Research Institute (IARI) to quantify the effect of elevated CO_2 and temperature on water use efficiency of two rice varieties viz. Pusa Basmati 1509 and Nagina 22. There were two different CO_2 concentrations i.e. ambient (410 ppm) and elevated (550 ± 25 ppm) and also two of rice different temperature levels i.e. ambient and elevated (+2.5-2.9°C). Results suggested that warming caused more accumulated GDD in rice, which negatively affected the duration of both the varieties. In elevated CO_2 plus high temperature interaction, net photosynthesis rate was more than that of control while stomatal conductance and transpiration rate got reduced. Hence the study showed that, co-elevation of CO_2 and temperature improved WUE (both instantaneous and intrinsic), of the crop.

Key words: Elevated CO_2, High temperature, Instantaneous WUE, Intrinsic WUE, Photosynthesis rate, Rice

The global climate is changing at an alarming rate due to the increasing emission of greenhouse gases (GHGs) such as carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O). In the pre-industrial era (1750 AD), the atmospheric CO_2 concentration was around 280 ppm; today, it is over 410 ppm (IPCC, 2021), mainly due to widespread anthropogenic activity, and it is anticipated to exceed 550 ppm by 2050 and 700 ppm by 2100 (Kumar *et al*., 2019). According to IPCC 6th assessment report, the temperature would likely rise by 1.5-5.0°C in mid of the scenario spectrum and by 3°C in 2100 (IPCC 2021). Warming and elevated CO_2 levels are having negative impacts on agricultural ecosystems, changing plant growth and food grain production in tropical and subtropical countries, including India (Chakrabarti *et al*., 2020; Guo *et al*., 2022; Singh, 2023). Significant evidence suggests that elevated CO_2 will stimulate photosynthesis rate and increase biomass production and yield, especially in C_3 crops (Saxena and Kumar, 2014; Brito *et al*., 2020; Lenka *et al*., 2021; Zhu *et al*., 2022). But rise in temperature along with increased CO_2 level will have certain harmful effect on crop plants. According to earlier studies (Cai *et al*., 2016; Wang *et al.,* 2016), warming reduced photosynthesis resulting in a decrease in crop biomass. Rise in temperature also shortens the crop growth duration leading to decreased productivity of the crop (Raj *et al.,* 2016; Das *et al.,* 2020).

Rice (*Oryza sativa* L.) is the second-most significant staple food crop in the world (Pathak *et al*., 2018). In India, rice occupies an area of nearly 43.8 million ha, with a total production of 177.6 million tonnes and productivity of 4,057 kg ha^{-1} (FAOSTAT, 2021). The primary effects of rising CO_2 on crops include an increase in photosynthetic rate, an improvement in water and light use efficiency, and a decrease in transpiration rate and stomatal conductance (Dey *et al.,* 2016). Although elevated CO_2 increases photosynthetic rate but it directly reduced leaf stomatal conductance by around 50%, lowering water losses and improving water use efficiency (WUE) (Ainsworth and Rogers, 2007; Pazzaglia *et al.,* 2016).Water use efficiency (WUE), or the amount of carbon gained

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per unit of water consumed, has emerged as a crucial indicator of how effectively water resources are utilized. Water Use Efficiency is the ratio of the amount of carbon assimilated through photosynthesis to the water lost via transpiration. This is also commonly known as instantaneous WUE (WUE_{inst}) (Farquhar and Richards, 1984). At the leaf level, water usage is regulated by the available energy reaching leaf, vapour pressure deficit, and aerodynamic exchange and also controlled by stomatal conductance of the plant (Hatfield and Dold, 2019). The intrinsic WUE (WUE_{intr}) is the ratio of net CO_2 assimilation through photosynthesis to stomatal conductance (Osmond *et al*., 1980). It has been suggested that breeding for high WUE by focusing on intrinsic WUE is possible (Condon *et al.,* 2004).

According to Qiao *et al.,* (2010), elevated CO_2 enhanced water use efficiency in C_3 crops. However, the amount of stomatal conductance that decreases in response to elevated CO_2 depends on the plant's condition, including its growth stage, as well as external factors like light and temperature (Bunce, 2004). There is currently relatively little evidence available on the interactive effect of elevated CO_2 and temperature rise on rice stomatal conductance, which might offer fresh insights into prospective agricultural interventions to decrease water use in the future.

MATERIALS AND METHODS

Experimental details

The study was conducted for two consecutive years (2019 and 2020) in *kharif* season (July to October) inside the Open Top Chamber (OTC) at the Genetic-H field of ICAR-Indian Agriculture Research Institute (IARI), New Delhi. The site is located at 28°37′ N latitude and 77°11′ E longitude at an altitude of 228.6 m above the mean sea level. The climate of the area is sub-tropical, semi-arid with hot summer and cool winter.

The OTCs were maintained at two different CO_2 concentrations viz. ambient (410 ppm) and elevated (550 ± 25 ppm) and two levels of temperature *i.e.,* ambient temperature and elevated temperature(+2.5-2.9°C). Elevated temperature was maintained by partially covering the upper portion of the OTCs with PVC shelter. Inside the OTCs the elevated CO_2 concentrations were maintained using a high pressurized CO_2 cylinders (of commercial grade 100% CO_2 of 30 kg capacity). Seedlings of two rice varieties namely Pusa basmati 1509 and Nagina 22 were transplanted in the crates inside the OTCs. Recommended dose of fertilizer *i.e.,* 120-60-60 (N-P_2O_5-K_2O) ($kg ha^{-1}$) was applied in rice crop.

Physiological and growth parameters

The number of days taken by each variety to reach the physiological maturity in each treatment were recorded through visual observations in the field. A portable photosynthesis system, InfraRed Gas Analyzer (IRGA Li-6400XT, Li-COR, USA) was used to record the gas exchange parameters viz. photosynthesis rate (Pn), stomatal conductance (g_s), transpiration rate (E) at the flowering stage of the crop. Leaf samples were collected at flowering stage. Leaf area was measured using LI-3100C Area Meter (LI-COR, Lincoln, NE). Observations on yield parameters were recorded after harvesting of plants.

Crop instantaneous WUE (WUE_{inst}) and intrinsic WUE (WUE_{intr}) were calculated from the above observations. The instantaneous WUE (WUE_{inst}) was calculated as the ratio of net photosynthesis (Pn) to the transpiration rate (E) and the intrinsic WUE (WUE_{intr}) was calculated as the ratio of net photosynthesis (Pn) to the stomatal conductance (g_s).

Computation of growing degree days (GDD)

Growing degree days (GDD) is one of agrometeorological indices used to quantify changes in the phenological behaviour and growth of crops under variable temperature (Kumar *et al*., 2010). The growing degree days (GDD) were calculated using the following formula provided by Nuttonson (1955).

$$GDD\ (°C\ day) = \frac{(T_{max} + T_{min})}{2} - T_b \quad \ldots\ldots\ldots\ldots (1)$$

Where, T_{max} = Daily maximum temperature (°C);

T_{min} =Daily minimum temperature (°C);

T_b = Base temperature, for rice it was taken as 10°C.

Statistical analysis

The design of the experiment was factorial CRD. Statistical analysis of the data was done using SAS (ver. 9.3) statistical package (SAS Institute Inc., CA, USA).

RESULTS AND DISCUSSION

Temperature elevation inside the Open Top Chambers (OTC)

In 2019 and 2020, mean seasonal temperature inside the chamber control treatment was 28.2 and 29.4°C respectively while mean seasonal temperature in elevated CO_2 plus temperature treatment was 31.0 and 32.4°C respectively.

Relationship between GDD and crop phenology

Physiological maturity of Pusa Basmati 1509 occurred 4 days earlier in both the years in elevated temperature treatment than chamber control. Maturity of Nagina 22 was earlier by 1 to 2 days in elevated temperature treatment than chamber control. Previous studies also showed that temperature rise accelerates the maturity of crops and thus reduces crop yield (Chakrabarti *et al*., 2021; Sandhu *et al.,* 2017).

Correlation analysis between GDD and crop duration showed that in both the varieties, increase in GDD had negative impact on crop duration (Fig. 1). GDD and crop duration were found to be negatively correlated and accumulation of more GDD in high temperature treatments reduced crop duration significantly. Chakrabarti *et al.,* (2021) also reported that crop growth period was shortened by the higher aggregated GDD for all growth phases in wheat crop. Among the two varieties Pusa Basmati 1509 showed more negative correlation with GDD and crop duration than Nagina 22.

Table 1: Effect of elevated CO_2 and temperature on photosynthesis rate (Pn), stomatal conductance (g_s) and transpiration rate (E) of both Pusa Basmati 1509 and Nagina 22 in 2019 and 2020: Experiments and the results of an analysis of variance (ANOVA). The main effects are CO_2, temperature (Temp.) and Varieties (Var.). Statistically significant differences are presented as (P <0.001, ***; P <0.01, **; P<0.05, *) and no statistical significance (P >0.05, ns).

		1st year			2nd year		
Treatment	Varieties	Pn	g_s	E	Pn	g_s	E
Chamber control	Pusa Basmati 1509	17.3b	0.31a	7.9a	19.5bc	0.36a	8.5a
	Nagina 22	12.8c	0.28ab	7.1abc	14.5de	0.29bcd	7.2bc
Elevated temperature	Pusa Basmati 1509	15.3b	0.30a	7.4ab	17.2cde	0.34ab	7.1bc
	Nagina 22	11.0c	0.29a	6.4bc	13.5e	0.28bcd	6.3c
Elevated CO_2	Pusa Basmati 1509	20.3a	0.28a	7.0abc	25.0a	0.31abc	7.3bc
	Nagina 22	16.6b	0.24b	6.1c	18.7bcd	0.22d	6.2c
Elevated CO_2 &temperature	Pusa Basmati 1509	19.9a	0.28ab	6.9abc	22.1ab	0.33abc	8.1ab
	Nagina 22	17.3b	0.24b	6.6bc	20.4abc	0.27cd	6.9bc
ANOVA	Factors						
	CO_2	***	**	ns	***	ns	ns
	Temperature	ns	ns	ns	ns	ns	ns
	Variety	***	**	*	**	***	**
	CO_2 X Temp.	ns	ns	ns	ns	ns	**
	CO_2 X Variety	ns	ns	ns	ns	ns	ns
	Temp. X Variety	ns	ns	ns	ns	ns	ns
	CO_2 X Temp. X Variety	ns	ns	ns	ns	ns	ns

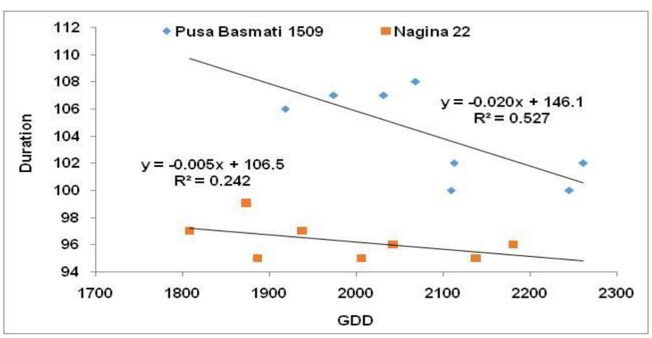

Fig 1: Correlation analysis between growing degree days (GDD) and crop duration of Pusa Basmati 1509 and Nagina 22

Effect of elevated CO_2 and temperature on rice physiology

Photosynthesis rate (Pn) ranged from 12.8 - 17.3 µmol CO_2 $m^{-2}s^{-1}$ during first year and from 14.5 - 19.5 µmol CO_2 $m^{-2}s^{-1}$ during second year (Table 1). Maximum photosynthesis rate was observed in Pusa Basmati 1509 (20.3 and 25 µmol CO_2 $m^{-2}s^{-1}$ in first and second year respectively) in elevated CO_2 and ambient temperature treatment. Elevated CO_2 significantly increased the photosynthesis rate in both the varieties. In elevated CO_2 plus high temperature treatment, photosynthesis rate was significantly higher than control.

A significant component in controlling the rate of photosynthesis and plant carbon metabolism is stomatal conductance (g_s), which influences the transport of CO_2 from the atmosphere to the stomatal cavity. Elevated CO_2 concentration of 550 ppm significantly reduced stomatal conductance in both the varieties while elevated temperature had no significant effect. In elevated CO_2 plus high temperature treatment, stomatal conductance of Pusa Basmati 1509 and Nagina 22 were 0.28 and 0.24 mol H_2O m^{-2} s^{-1} during first year and 0.33 and 0.27mol H_2O m^{-2} s^{-1}during second year of study (Table 1). Similar observation was made by Zhang *et al.,* (2022), who reported that elevated CO_2 alone and elevated CO_2 plus temperature interaction reduced stomatal conductance in rice. However, earlier research found that the impact of warming on stomatal conductance could be either positive or negative (Lahr *et al*., 2015; Urban *et al.,* 2017).

Transpiration rate (E) was found to be highest in chamber control treatment in both the varieties. In chamber control treatment transpiration rate of Pusa Basmati 1509 and Nagina 22 was 7.9 and 7.1 mmol H_2O m^{-2} s^{-1} respectively during first year and 8.5 and 7.2 mmol H_2O $m^{-2}s^{-1}$ respectively during second year of study (Table 1). Transpiration rate of both the varieties reduced in elevated CO_2 plus high temperature treatment. Zhang *et al.,* (2022) also reported that elevated CO_2 and warming significantly reduced transpiration rate in rice throughout the growth period as compared to control. Apple *et al.,* (2000) and Dwivedi *et al.,* (2022) also found that elevated CO_2 negatively induce transpiration rate.

Effect of elevated CO_2 and temperature on water use efficiency in rice

Elevated CO_2 increased both instantaneous and intrinsic

Table 2: Effect of elevated CO_2 and temperature on WUE_{inst}(instantaneous WUE) (µmol CO_2 $mmol^{-1}$ H_2O) and WUE_{intr} (intrinsic WUE) (µmol CO_2 mol^{-1} H_2O) of both Pusa Basmati 1509 and Nagina 22 in 2019 and 2020: Experiments and the results of an analysis of variance (ANOVA).The main effects are CO_2, temperature and Varieties. Statistically significant differences are presented as ($P < 0.001$, ***; $P < 0.01$, **; $P < 0.05$, *) and no statistical significance ($P > 0.05$, ns).

		1st year		2nd year	
Treatment	Varieties	WUE_{inst}	WUE_{intr}	WUE_{inst}	WUE_{intr}
Chamber control	Pusa Basmati 1509	2.2 bcd	56.8 bc	2.3 bc	54.9 b
	Nagina 22	1.8 d	46.7 c	2.0 c	50.3 b
Elevated temperature	Pusa Basmati 1509	2.1 cd	50.4 c	2.5 bc	50.3 b
	Nagina 22	1.7 d	48 c	2.2 bc	49.3 b
Elevated CO_2	Pusa Basmati 1509	2.9 a	71.8 a	3.6 a	84.4 a
	Nagina 22	2.7 ab	68.7 ab	3 ab	86.3 a
Elevated CO_2&temperature	Pusa Basmati 1509	2.9 a	71.5 a	2.7 abc	67.6 ab
	Nagina 22	2.6 abc	71.5 a	2.9 ab	77.6 ab
ANOVA	**Factors**				
	CO_2	***	***	**	***
	Temperature	ns	ns	ns	ns
	Variety	*	ns	ns	ns
	CO_2 X Temp.	ns	ns	ns	ns
	CO_2 X Variety	ns	ns	ns	ns
	Temp. X Variety	ns	ns	ns	ns
	CO_2 X Temp. X Variety	ns	ns	ns	ns

WUE in the rice varieties. WUE_{inst} of Pusa Basmati 1509 has increased under elevated CO_2 as compared to chamber control from 2.2 to 2.9 µmol CO_2 $mmol^{-1}$ H_2O during first year and from 2.3 to 3.6 µmol CO_2 $mmol^{-1}$ H_2O during second year of study. Similarly, WUE_{inst} has increased from 1.8 to 2.7 µmol CO_2 $mmol^{-1}$ H_2O in first year and 2.0 to 3.0 µmol CO_2 $mmol^{-1}$ H_2O in second year in Nagina 22 (Table 2). Our findings concur with those of Ruiz-Vera *et al*., (2013) and Li *et al*., (2019) who concluded that WUE increased under high CO_2 conditions. Instantaneous WUE increased by 19 to 29% in Pusa Basmati 1509 and by 44 to 47% in Nagina 22 variety under elevated CO_2 plus temperature treatment than chamber control Zhang *et al.,* (2022) also reported that except at anthesis stage, under elevated CO_2 plus temperature condition instantaneous WUE of rice leaves showed an increasing trend due to reduced stomatal conductance at elevated CO_2 condition.

WUE_{intr} of Pusa Basmati 1509 and Nagina 22 has also increased from 56.8 and 46.7 to 71.8 and 68.7 µmol CO_2 mol^{-1} H_2O respectively in first year under elevated CO_2 treatment as compared to chamber control (Table 2). Similar trend was also followed in second year. According to Oiao *et al*., (2010), WUE enhanced under elevated CO_2 condition due to increased carbon assimilation efficiency and decreased stomatal conductance and transpiration in C_3 crops. Similar to instantaneous WUE, intrinsic WUE of Pusa Basmati 1509 and Nagina 22 was also observed to be increased by 26 and 53 % respectively in first year and 23 and 54 % in second year under elevated CO_2 plus temperature as compared to control. This might be due to the fact that plant net photosynthesis rate of rice was significantly higher while stomatal conductance reduced under elevated CO_2 plus temperature condition. Percent increase of both instantaneous and intrinsic WUE has observed to be higher in Nagina 22 in both years as compared to Pusa Basmati 1509. Nagina 22, being a heat tolerant variety, exhibited more resistance towards temperature rise than Pusa Basmati 1509. Increased WUE also suggests that the genotype may be able to maintain a high rate of carbon assimilation under stress condition or may be elevated CO_2 concentration may have amelioration effect (Hatfield and Dold, 2019).

Multiple correlations between these variables provide additional support for our findings. Results showed that photosynthesis rate is highly correlated (positive) with both instantaneous WUE (r= 0.89, p-value<0.001) and intrinsic WUE (r= 0.81, p-value<0.001). This indicates that higher photosynthesis rate enhance WUE due to increased carbon assimilation by plant. Stomatal conductance and transpiration rate are positively correlated (r= 0.82, p-value<0.001) and both of them are also negatively correlated with both instantaneous and intrinsic WUE. This suggests that lower stomatal conductance under elevated CO_2 further reduced plant water loss through transpiration which eventually enhance plant WUE. The negative correlation of both WUE_{inst} and WUE_{intr} with stomatal conductance and transpiration rate is in agreement with Li *et al.,* (2017) and Abdelhakim *et al.,* (2021).

CONCLUSION

The findings of this study suggest that elevated temperature caused more accumulated GDD in rice and accelerated the maturity of the crop. Co-elevation of CO_2 and temperature, has also improved WUE through enhanced carbon assimilation and decreased stomatal conductance and transpiration in rice crop. According to the results of this study, rice displays genotypic variations in photosynthetic potential under co-elevation of CO_2 and temperature. Therefore, it is essential to investigate a wider range of varieties in order to increase our understanding level on how climate change affects rice crop. This can potentially help in developing improved varieties with enhanced yield and WUE under CO_2 and temperature condition.

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***Data availability statement*:** Data available on reasonable request from the authors.

Authors contribution: **P. P. Maity**: Conducting the experiment, data collection, sample analysis, and manuscript writing; **B. Chakrabarti**: Planning the experiment, interpretation of data, and manuscript writing; **A Bhatia**: Data interpretation, editing of manuscript; **SN Kumar**: Facilitating and planning the experiment; **TJ Purakayastha**: Data interpretation; **D Chakraborty:** Editing of manuscript; **S Adak**: Data analysis; **A Sharma**: Conducting the experiment, collection of samples from field; **S Kannojiya**: Sample analysis.

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