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Combined effects of elevated air temperature and CO_2 on growth, yield, and yield components of japonica rice (*Oryza sativa* L.)

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Abstract

In the region where heat stress has become evident, the elevation of air temperature could reduce yield of heat stress-susceptible crops, such as rice (*Oryza sativa* L.), which is a major food staple in Asia. In addition to air temperature, atmospheric CO_2 is projected to be elevated in the future. To project rice yield in the future, it is necessary to clarify the responses of rice to concurrent elevations of air temperature and atmospheric CO_2. In the present study, two japonica rice cultivars with different heat tolerance, Hinohikari (sensitive) and Nikomaru (tolerant), were grown in pots inside open-top chambers and exposed to elevated air temperature and/or CO_2. The degrees of increase in the air temperature and CO_2 concentration by the treatments were approximately 1 °C and 120 μmol mol^{-1} (ppm). The study was conducted in Nagasaki, Japan, where heat stress on rice has become evident. Elevated air temperature significantly decreased both whole-plant growth and grain yield. Elevated CO_2 significantly increased the growth but significantly decreased the yield. The effects of elevated air temperature and elevated CO_2 on growth and yield did not significantly differ between two cultivars. In both cultivars, the main cause of yield reduction by both treatments was reduction in spikelet fertility, which is typical heat stress on rice. The elevated CO_2-induced reduction in spikelet fertility could be explained partially by high-temperature regime during flowering due to acceleration of heading and by increase in canopy temperature via stomatal closure in flag leaves. Because elevated air temperature and elevated CO_2 treatments additively reduced spikelet fertility in both cultivars, concurrent elevations of air temperature and CO_2 caused considerable reduction in grain yield.

Keywords Elevated CO_2, Heat stress, Japonica rice, Open-top chamber, Stomatal conductance

1 Introduction

Global mean surface temperature has risen (Gulev et al., 2021) and is projected to rise in the future based on socioeconomic and greenhouse gas emission scenarios (Lee et al., 2021). Elevation of air temperature adversely affects the yield of heat stress-susceptible crops, such as rice (*Oryza sativa* L.), which is a major food staple in Asia (OECD/FAO, 2022). The typical effects of heat stress on rice are reduced spikelet fertility and deteriorated grain quality (Jagadish et al., 2015; Morita et al., 2016). In Japan, the effects of heat stress on rice, such as deteriorated grain appearance quality, have become evident in the Kyushu region, which is a warm temperate

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area located in western Japan (Ishigooka et al., 2011; Okada et al., 2009). In this region, it is projected that further reduction in grain quality of rice could occur in the future because of increased air temperature, although the degree of deterioration depends on future climate scenarios and heat tolerance of cultivars (Okada et al., 2011; Kinose and Seita, 2022). Therefore, heat stress on rice cultivated in this region will become evident in the future.

In addition to the global mean surface temperature, atmospheric carbon dioxide (CO_2) concentration has risen (Gulev et al., 2021) and is projected to rise in the future (Canadell et al., 2021). Although an elevation of atmospheric CO_2 concentration generally enhances plant growth and crop production because photosynthesis is a CO_2-dependent process (Körner, 2003), the degree of enhancement differed among crops, cultivars, and growth conditions (Ainsworth, 2008; Ainsworth & Long, 2021; Hasegawa et al., 2013). In rice, Ainsworth (2008) reported that elevated CO_2 (+262 ppm) increased rice yield by 23%, although the degree of yield increase varied depending on the magnitude of the elevation and fumigation technique. Hasegawa et al. (2013) reported that the increase in rice yield by elevated CO_2 exposure considerably differed among the cultivars and was greater in the cultivars with a large sink capacity. Furthermore, Ainsworth and Long (2021) conducted meta-analysis of free-air CO_2 enrichment (FACE) experiments and reported that warming reduced the elevated CO_2-induced increase in yield of C_3 crops, including rice. These results indicate that the effects of elevated CO_2 on rice yield could differ due to elevated air temperature and among cultivars.

Several researchers have suggested that elevated CO_2 exacerbated heat-induced reduction in spikelet fertility of japonica and indica rice cultivars (Kim et al., 1996; Kobayasi et al., 2019; Matsui et al., 1997). Hasegawa et al. (2016) conducted FACE experiments and reported that exposure to elevated CO_2 reduced spikelet fertility of the japonica rice cultivar in warm years. Reduced spikelet fertility decreases rice yield regardless of whole-plant growth because it is related to harvest index reduction (Prasad et al., 2006). Therefore, because of possible reduction in spikelet fertility caused by elevated CO_2, rice yield could be less than that predicted by considering growth enhancement due to the elevated CO_2, especially in region where heat stress has become evident, such as Kyushu, Japan. However, there is no information on how concurrent elevations of air temperature and CO_2 affect growth, yield, and yield components including spikelet fertility of rice cultivated in this region.

In our previous study, two japonica rice cultivars with different heat tolerance regarding grain quality, Hinohikari (sensitive) and Nikomaru (tolerant), were exposed to elevated CO_2 using open-top chambers (OTCs) in Nagasaki, Kyushu (Yamaguchi et al., 2022), where heat stress on rice has become evident (Ishigooka et al., 2011; Okada et al., 2009). We reported that the exposure to elevated CO_2 significantly increased whole-plant growth, but did not significantly affect yield by reducing spikelet fertility in both cultivars. These results suggest that concurrent elevations of air temperature and CO_2 could considerably reduce yield via reduction in spikelet fertility especially in region where heat stress has become evident. Therefore, to clarify combined effects of elevated air temperature and elevated CO_2 on rice yield in the region, we conducted an experimental study on the combined effects on growth, yield, and yield components of two japonica rice cultivars with different heat tolerance using OTCs in Kyushu, Japan.

2 Materials and methods

2.1 Plant material

On 7 June 2019, the seedlings of two japonica rice cultivars, "Hinohikari" and "Nikomaru," were planted in 1/5000 a Wagner's pots (ø159 mm × 300 mm in height, approximately 6 L) filled with a flooded mixture of Andisol and Akadama soils (1:1) in three hills per pot; two seedlings were included per hill. Before planting, 3.33 g of N-P-K fertilizer (N-P-K = 15:15:15) (250 kg N ha^{-1}) and silica fertilizer (15.0 g) were applied to the pots as a basal dressing. The plants were cultivated in 16 OTCs (60 cm in width, 120 cm in height, and 82.5 cm in length) located at Nagasaki University (Nagasaki, Japan; 32.79 N, 129.87 E) (Yamaguchi et al., 2022). Inside each OTC, ambient air was introduced using a fan (MRS18V2-B, Oriental Motor Co., Ltd., Tokyo, Japan) and blown in an upward direction from the bottom of the chamber.

The seedlings were assigned to the OTCs on 28 June and cultivated until 11 October. On 8 August, 1.67 g of the N-P-K fertilizer (125 kg N ha^{-1}) was applied to each pot as a top dressing. Irrigation was conducted to keep the soil flooded during the cultivation period. The air temperature (T_{air}) and relative humidity (RH) in the OTCs were continuously measured using a TR-72-wf Thermo Recorder (T&D Corporation, Nagano, Japan) as described in Yamaguchi et al. (2022). The T_{air} and RH on 12 and 24 July and 8 August were missing due to data acquisition and maintenance. Mean hourly global solar radiation from 29 June to 11 October was 176 W m^{-2}, which was measured at the Nagasaki Local Meteorological Observatory, approximately 5.8 km south of the experimental site, and is available at the Japan Meteorological Agency website (https://www.data.jma.go.jp/gmd/risk/obsdl/index.php).

2.2 Elevated air temperature and elevated CO_2 treatment

This experiment had a split-plot factorial design and employed the randomized block method. The whole-plot treatment included two levels of air temperature and two levels of CO_2 with four chamber replicates for a total of 16 OTCs that could be analyzed. The sub-plot treatments consisted of two cultivars in each OTC. Three pots (i.e., nine hills) for each cultivar (six total pots) were placed in each OTC. The rice plants were exposed to elevated air temperature and elevated CO_2 treatments from June 29 to October 11.

Ambient air was introduced into the four OTCs assigned to the control treatment. Four OTCs assigned to the elevated air temperature (E-Temp) treatment were equipped with an air heating system that consisted of two silicon belt heaters (150 W, SBH-115, Sakaguchi E.H Voc Corp., Tokyo, Japan) and a radiation-heated black tube. CO_2 gas was introduced into the four OTCs assigned to the elevated CO_2 (E-CO_2) treatment. The other four OTCs were assigned to the elevated air temperature and CO_2 (E-Temp/E-CO_2) treatment, in which introduced air was heated by the heating system, and CO_2 gas was introduced into the OTCs. The target CO_2 concentration in the E-CO_2 treatment was ambient plus 150 μmol mol^{-1} (ppm) during the day from before sunrise until after sunset.

Table 1 shows the T_{air} and RH from 29 June to 11 October 2019. T_{air} was increased by E-Temp treatment by approximately 1 °C, which resulted in lower RH. The hourly maximum T_{air} exceeded 40 °C in the E-Temp and E-Temp/E-CO_2 treatments, but did not in the control and E-CO_2 treatments. Figure 1 depicts the time course of hourly air temperature in the control, E-CO_2, E-Temp, and E-Temp/E-CO_2 treatments. When rice is exposed to temperatures higher than 35 °C, high-temperature injuries occur according to growth stages (Yoshida, 1981). Because of this, we counted the hourly air temperature higher than 35 °C for each treatment. In total, 101 h exceeded 35 °C in the control and E-CO_2 treatments, and 216 h exceeded 35 °C in the E-Temp and E-Temp/E-CO_2 treatments.

The regulation and measurement of CO_2 concentration inside the OTCs assigned to the E-CO_2 and E-Temp/E-CO_2 treatments were described in Yamaguchi et al. (2022). The mean CO_2 concentration inside the OTCs assigned to the E-CO_2 and E-Temp/E-CO_2 treatments during the day from 29 June to 22 September was 545 ± 10 ppm (mean of eight chambers ± standard deviation). The CO_2 concentration in the ambient air from 29 June to 22 September was 427 ppm. From 22 September to 11 October, we did not measure the CO_2 concentration because of machine trouble, but we continued introducing CO_2 gas into the OTCs at the same flow rate of CO_2 gas injection into the OTCs to maintain the elevated CO_2 treatment at the same magnitude as before 22 September.

2.3 Stomatal conductance and plant canopy temperature

On 30 August, which was immediately after and during the flowering period for about 5 days around heading date of Hinohikari and Nikomaru, respectively, we measured stomatal conductance (g_s) in the flag leaves using the steady-state diffusion porometer (Leaf Porometer Model SC-1, METER Environment, Pullman, WA, USA). The measurements were made inside the OTCs from 11:00 a.m. to 12:00 a.m.

For each cultivar, two or three hills from each OTC were randomly selected for the measurements. Simultaneously, to measure plant temperature in the canopy, we took infrared images of the rice plant canopy inside each OTC using an infrared thermal imaging camera (FLIR i5, Teledyne FLIR LLC, Wilsonville, OR, USA). Because it was difficult to identify the plant organs in the infrared image, we analyzed the minimum temperature within the range of the canopy that could be easily distinguished in the OTC. Although the minimum temperature is not representative of the canopy temperature, we assumed that

Table 1 Air temperature (T_{air}) and relative humidity (RH) in each treatment from 29 June to 11 October 2019

Treatment	T_{air} (°C)					RH (%)		
	Periodical mean			Hourly	Hourly	Periodical mean		Hourly
	Daily mean	Daily max.[a]	Daily min.[b]	Max	Min	Daily mean	Daily min.[b]	Min
Control	26.9	31.5	23.6	39.2	14.5	77.8	59.4	24.3
E-Temp	28.0	33.0	24.9	41.3	15.3	73.1	53.9	24.7
E-CO_2	27.1	32.0	23.6	38.9	14.9	75.5	55.6	24.7
E-Temp/E-CO_2	28.1	33.3	24.4	40.9	15.4	71.7	52.2	23.5

Each value shows the mean of four chambers for each treatment ($n = 4$)

[a] Mean of daily 1-h maximum value

[b] Mean of daily 1-h minimum value

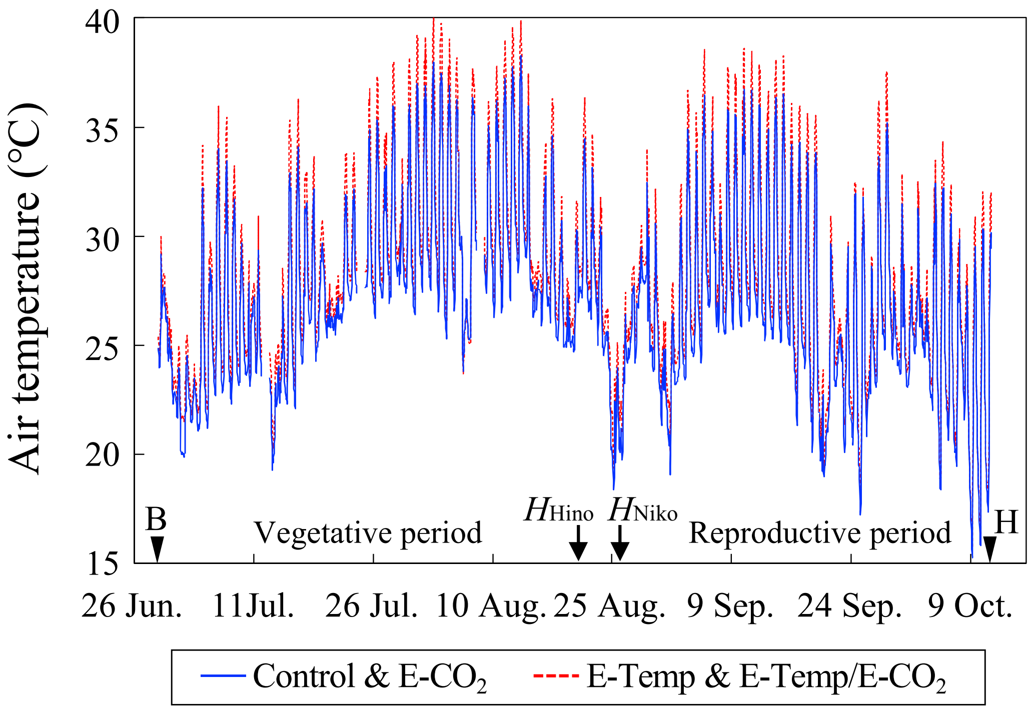

Fig. 1 Time course of hourly air temperature inside open-top chambers during the experimental period from 29 June to 11 October 2019. Each value shows the mean of 8 chambers assigned to the control and elevated CO_2 treatments (control & E-CO_2, solid blue line) or the elevated air temperature and elevated air temperature and elevated CO_2 treatments (E-Temp & E-Temp/E-CO_2, dotted red line). Arrowheads indicate beginning of the treatment (B) and final harvest (H). Arrows indicate the heading dates of Hinohikari and Nikomaru in the control (H_{Hino} and H_{Niko}, respectively)

the minimum temperature in the images would be plant temperature, and, by comparing temperatures among treatments, we could identify effects of the treatments on plant temperature. Because we were unable to distinguish the cultivars in this analysis, it is unclear if measured minimum temperatures were from Hinohikari or Nikomaru. However, by comparing the minimum plant canopy temperatures among the treatments, we could clarify the effects of elevated air temperature and/or elevated CO_2 on plant temperature at the beginning of the reproductive period.

2.4 Growth, yield, and yield components

From 17 August to 8 September, stem and panicle numbers were measured every day to determine the heading date. The heading date was defined as the day on which the mean heading rate reached 50% for each treatment and each cultivar. We calculated the mean daily T_{air} during the flowering period for 5 days around heading date (T_{mean}), mean daily maximum T_{air} for 3 days after heading date (T_{max}), and daily mean T_{air} 9 days before heading (T_{BH}). To determine the dry mass (DM) of plant organs and the yield and yield components, all rice plants of both Hinohikari and Nikomaru cultivars were harvested from each hill on 8 and 11 October 2019, respectively. The harvested plants were divided into panicles, leaf blades, stems (including leaf sheaths), and root parts. All plant organs except for the panicle were dried in an oven at 80 °C for 5 days and weighed. The panicles were counted to obtain the panicle number per hill and air-dried in the field for 5 days. Whole-plant DM per hill was calculated as the sum of the DM of all plant organs.

Spikelets were separated from dried panicles and counted to obtain the spikelet number per panicle. The spikelets were manually categorized into two groups, sterile and fertile, and counted. Fertile spikelets consist of filled and partially filled spikelets. To evaluate spikelet fertility, the percentage of fertile spikelets was calculated from the total and fertile spikelet numbers for each hill. Fertile spikelets were weighed to obtain the yield per hill, and the 1000-grain mass was calculated using the fertile spikelet number per hill. Since there were few partially filled spikelets, we defined the mass of fertile spikelets per hill as yield per hill.

2.5 Statistical analysis

The mean of three pots (i.e., nine hills) for each OTC was used for statistical analyses ($n=4$ for each treatment). A three-way analysis of variance (ANOVA) was used to test the effects of the elevated air temperature (T), elevated

CO_2, and cultivar. The three-way ANOVA results are shown in Table 2. When there was a significant interaction between cultivar and T or CO_2, we used a two-way ANOVA to identify the significant effects of T and CO_2 for each cultivar. When there was a significant interaction between T and CO_2, Tukey's HSD test was used to identify significant differences among the four treatments for each cultivar. The spikelet fertility was analyzed after logit transformation. For air temperature during the flowering period and canopy plant temperature, two-way ANOVA was used to test T, CO_2, and their interaction. All statistical analyses were performed using IBM SPSS Advanced Statistics 22 (IBM Japan, Ltd., Tokyo, Japan).

3 Results and discussion

3.1 Different responses of growth and yield

Figure 2 and Table 2 show the combined effects of elevated air temperature and elevated CO_2 on whole-plant DM and yield of two japonica rice cultivars, Hinohikari and Nikomaru, and the associated statistical significance. Whole-plant DM and yield were significantly reduced by the E-Temp treatment (Fig. 2a, b). Although there was significant interaction between E-Temp and cultivar for the yield, the degree of reduction in the yield by the elevated air temperature treatment did not differ between the cultivars. When rice is exposed to temperatures higher than 35 °C, high-temperature injuries occur based on growth stages (Yoshida, 1981). In this study, the number of hours in which T_{air} exceeded 35 °C was doubled by the E-Temp treatment (Fig. 1). Therefore, in the E-Temp treatment, high-temperature stress caused reductions in whole-plant growth and yield. Significant reductions in growth and yield were induced by increase in mean T_{air} by only 1 °C (Table 1), and there were more than 100 h in which T_{air} exceeded

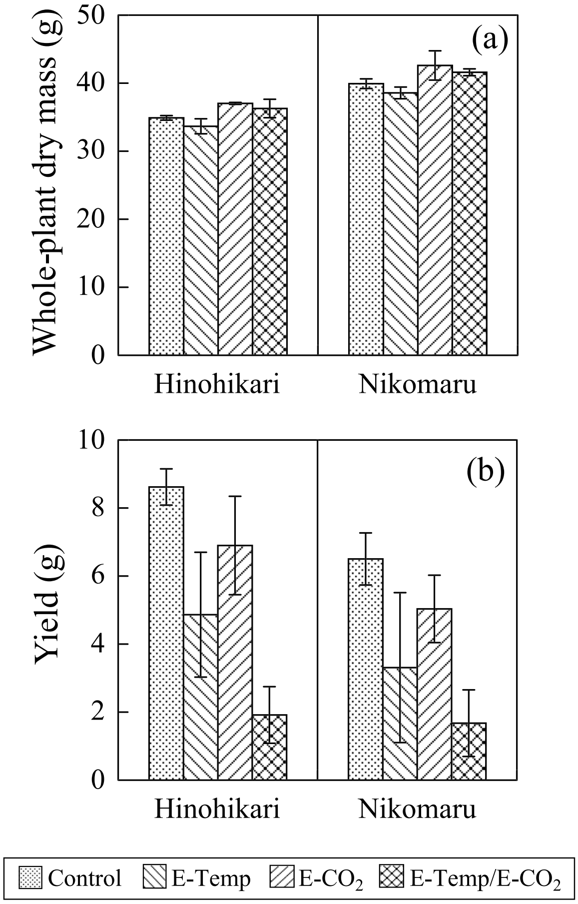

Fig. 2 Effects of elevated air temperature and elevated CO_2 on whole-plant dry mass (**a**) and yield (**b**) of two Japanese rice cultivars (*Oryza sativa* L., cvs. Hinohikari and Nikomaru) in October 2019. Each value shows the mean of four chamber replications ($n=4$), and each standard deviation is shown by a vertical bar. Three-way ANOVA results are shown in Table 2

Table 2 Three-way ANOVA results of the effects of elevated air temperature (T), elevated CO_2 (CO_2), and cultivar (Cv) on whole-plant dry mass, yield, yield components, and stomatal conductance

Source	Whole-plant dry mass	Yield	Panicle no. per plant	Floret no. per panicle	1000-grain mass	Spikelet fertility	Stomatal conductance
T	*	***	n.s.	n.s.	**	***	n.s.
CO_2	***	***	n.s.	n.s.	n.s.	***	***
$T \times CO_2$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Cv	***	***	***	***	*	***	n.s.
T × Cv	n.s.	*	n.s.	n.s.	*	n.s.	n.s.
$CO_2 \times$ Cv	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.
$T \times CO_2 \times$ Cv	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

n.s. not significant

[*] $p < 0.05$

[**] $p < 0.01$

[***] $p < 0.001$

35 °C in the control treatment (Fig. 1). Therefore, the T_{air} of the control treatment was equivalent to or higher than optimal for rice growth.

Exposure to elevated CO_2 significantly increased whole-plant DM but significantly reduced yield (Fig. 2a, b and Table 2). In Hinohikari, whole-plant DM was significantly less, and the yield was significantly higher than Nikomaru. Because there were no significant interactions between E-CO_2 and E-Temp or cultivar for the whole-plant DM and yield, the effect of E-CO_2 on the whole-plant DM and yield was not significantly modified by E-Temp and did not significantly differ between the cultivars. Furthermore, there were no significant interactions among elevated air temperature, elevated CO_2, and cultivar for the whole-plant DM and yield (Table 2). This result indicates that the combined effects on growth and yield were additive, and growth and yield responses to both treatments did not significantly differ between Hinohikari and Nikomaru. On average across the cultivars, there were −2.8% and +7.1% changes in whole-plant DM caused by E-Temp and E-CO_2 treatments, respectively. In the E-Temp/E-CO_2 treatment, the whole-plant DM was somehow higher than that in the control treatment. On the other hand, yield reduction by E-Temp and E-CO_2 treatments was 46.0% and 21.1%, respectively, on average across the cultivars. Furthermore, because both treatments additively reduced yield, the yield in the E-Temp/E-CO_2 treatment was 76.3% lower than that in the control treatment, on average across the cultivars.

3.2 Effects on yield components and their contribution to yield reduction

To understand how E-Temp and E-CO_2 treatments caused yield reduction, we measured the yield components of rice (Tables 2 and 3). Although panicle number per plant of Hinohikari was significantly lower than that of Nikomaru, there were no significant effects of either treatment and their significant interactions on the panicle number per plant. For floret number per panicle, on the contrary, the number of Hinohikari was significantly higher than that of Nikomaru. Furthermore, significant interaction of elevated CO_2 and cultivar was observed in floret number per panicle. Two-way ANOVA revealed that elevated CO_2 significantly increased floret number per panicle in Nikomaru, but not in Hinohikari (Table 3). There were significant main effects of E-Temp and cultivar and their interaction for 1000-grain mass. Two-way ANOVA revealed that elevated air temperature significantly reduced 1000-grain mass of Hinohikari, but not of Nikomaru (Table 3). This cultivar difference could be caused by heat tolerance of Nikomaru compared with Hinohikari (Tanaka et al., 2009; Tanamachi et al., 2016).

Spikelet fertility was significantly reduced by the E-Temp and E-CO_2 treatments without their interaction (Table 2). Although the spikelet fertility of Hinohikari was significantly higher than that of Nikomaru, reduction in the spikelet fertility by the E-Temp and E-CO_2 treatments and their combination did not significantly differ between the cultivars. These results indicate that the yield reductions due to elevated air temperature,

Table 3 Combined effects of elevated air temperature (E-Temp) and elevated CO_2 (E-CO_2) treatments on yield components of two rice cultivars in October 2019

Cultivar	Treatment		Panicle no. per plant	Floret no. per panicle	1000-grain mass (g)	Spikelet fertility (%)
Hinohikari	Control		7.0 (0.2)	67.6 (0.8)	23.9 (0.8)	76.6 (3.5)
	E-Temp		7.1 (0.3)	67.7 (2.2)	21.1 (0.9)	46.9 (18.2)
	E-CO_2		7.3 (0.3)	66.3 (0.6)	23.8 (0.2)	60.4 (11.1)
	E-Temp/E-CO_2		7.2 (0.3)	68.1 (3.9)	19.5 (1.2)	19.5 (8.2)
	Two-way	Temp (T)	-	n.s.	***	-
	ANOVA	CO_2	-	n.s.	n.s.	-
		T×CO_2	-	n.s.	n.s.	-
Nikomaru	Control		7.7 (0.2)	61.3 (1.1)	24.3 (1.3)	57.2 (6.6)
	E-Temp		7.7 (0.3)	59.3 (3.1)	24.7 (3.7)	31.6 (20.9)
	E-CO_2		7.6 (0.4)	64.9 (1.0)	23.7 (0.5)	42.6 (6.0)
	E-Temp/E-CO_2		7.6 (0.2)	62.5 (1.7)	21.1 (1.3)	16.4 (9.2)
	Two-way	Temp (T)	-	n.s.	n.s.	-
	ANOVA	CO_2	-	*	n.s.	-
		T×CO_2	-	n.s.	n.s.	-

Each value is the mean of four chambers ($n=4$), and its standard deviation is shown in parentheses. Two-way ANOVA was used to identify the significant effects of temperature (T) and CO_2 for each cultivar, only when there was a significant interaction between cultivar and T or CO_2 according to the result of three-way ANOVA (Table 2). Two-way ANOVA: $^{*}p < 0.05$, $^{***}p < 0.001$, *n.s.* not significant. -not conducted elevated CO_2, and their combination were mainly caused by reduction in spikelet fertility in both cultivars. In addition, the yield reduction due to elevated air temperature in the heat-sensitive cultivar Hinohikari was partially exacerbated by reduction in 1000-grain mass, and that due to elevated CO_2 in heat-tolerant cultivar Nikomaru was partially ameliorated by increase in floret number per panicle, although both exacerbation and amelioration could be marginal effect on the grain yield. Furthermore, the combined effects of elevated air temperature and elevated CO_2 on the yield components were additive in both cultivars, which resulted in considerable yield reduction in the E-Temp/E-CO_2 treatment.

Table 4 Heading date and mean air temperature during 5 days around the heading date (T_{mean}), mean daily maximum air temperature for 3 days after the heading date (T_{max}), and daily mean air temperature in 9 days before the heading date (T_{BH}) in each treatment

Cultivar	Treatment	Heading date	T_{mean}	T_{max}	T_{BH}
Hinohikari	Control	21 Aug	27.5 (0.1)	32.4 (0.5)^b	31.8 (0.4)^c
	E-Temp	22 Aug	28.4 (0.2)	30.9 (0.4)^c	33.8 (0.5)^a
	E-CO_2	20 Aug	27.8 (0.2)	33.0 (0.4)^b	31.6 (0.3)^c
	E-Temp/E-CO_2	20 Aug	28.7 (0.3)	34.4 (0.6)^a	32.6 (0.2)^b
	Two-way	Temp (T)	***	n.s.	***
	ANOVA	CO_2	*	***	**
		T×CO_2	n.s.	***	*
Nikomaru	Control	26 Aug	24.1 (0.3)^b	27.7 (0.2)^b	29.1 (0.2)^c
	E-Temp	26 Aug	25.2 (0.2)^a	28.9 (0.1)^a	30.5 (0.3)^a
	E-CO_2	24 Aug	24.8 (0.2)^a	25.5 (0.3)^d	27.3 (0.1)^d
	E-Temp/E-CO_2	25 Aug	25.2 (0.4)^a	27.1 (0.2)^c	29.7 (0.2)^b
	Two-way	Temp (T)	***	***	***
	ANOVA	CO_2	n.s.	***	***
		T×CO_2	*	*	***

Each value is the mean of four chambers ($n=4$), and its standard deviation is shown in parentheses. Two-way ANOVA: $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$, *n.s.* not significant. Values with different letters are significantly different at $p<0.05$ (Tukey's HSD test)

3.3 Air temperature during the flowering period

Spikelet fertility is most sensitive to high temperatures at heading and at approximately 9 days before heading (Yoshida, 1981). Maruyama et al. (2013) reported function of spikelet fertility reduction using mean daily maximum air temperature for 3 days after heading date. Because elevated air temperature and elevated CO_2 can accelerate heading (e.g., Oh-e et al., 2007; Yamaguchi et al., 2022), we compared the temperature regime during the flowering period around the heading date (Table 4). In Hinohikari, compared with the control treatment, the heading date was delayed 1 day in the E-Temp treatment and accelerated 1 day in the E-CO_2 and E-Temp/E-CO_2 treatments. Compared with the control treatment, T_{mean} and T_{BH} were significantly high in the E-temp treatment due to the elevated air temperature treatment and E-Temp-induced delay in heading date. The T_{max} in the E-Temp treatment was significantly low due to heading delay, because the air temperature in the control treatment during the calculation period for T_{max} in the E-Temp treatment from 22 to 24 August was less than that in the control treatment from 21 to 23 August. These results indicate that the averagely higher temperature regime during the flowering period and before heading could cause E-Temp-induced reduction in spikelet fertility in Hinohikari. There were no significant differences in T_{max} and T_{BH} between the control and the E-CO_2 treatments. In the E-CO_2 treatment, however, T_{mean} was significantly higher than that in the control by 0.3 °C due to accelerating heading date, because daily mean air temperature in the control treatment in 18 August, which was included in calculation period for T_{mean} in the E-CO_2 treatment but was not in the control treatment, was higher than that in 23 August, which was included in calculation period for T_{mean} in the control treatment but was not in the E-CO_2 treatment. Therefore, T_{mean} increase could partially cause E-CO_2-induced reduction in spikelet fertility, but the drastic reduction in spikelet fertility of more than 10% could not be completely explained by this increase. In the E-Temp/E-CO_2 treatment, T_{max} was significantly higher, and T_{BH} was significantly lower than those in the E-temp treatment by 3.5 °C and 1.2 °C, respectively. The T_{max} increase could explain the further reduction in spikelet fertility than that in the E-Temp treatment by exposure to elevated CO_2 under elevated air temperature.

In Nikomaru, compared with the control treatment, the heading date accelerated by 2 and 1 days in the E-CO_2 and E-Temp/E-CO_2 treatments, respectively. There were significant interactions between E-Temp and E-CO_2 for T_{mean}, T_{max}, and T_{BH}. In the E-temp treatment, T_{mean}, T_{max}, and T_{BH} were significantly higher than those in the control treatment due to elevated air temperature treatment, because the calculation periods for the parameters were same between the control and E-Temp treatments. Therefore, the low spikelet fertility in the E-Temp treatment could be caused by the high-temperature regime during both the flowering period and before heading. In the E-CO_2 treatment, compared with the control treatment, T_{max} and T_{BH} were significantly low by 2.2 °C and 1.8 °C, respectively. However, T_{mean} in the E-CO_2 treatment was significantly high by 0.7 °C as compared with the control treatment due to acceleration of heading date, because mean air temperature in the control treatment on 22 and 23 August, which were included in calculation period for T_{mean} in the E-CO_2 treatment but were not in the control treatment, was higher than that in 27 and 28 August, which were included in calculation period for T_{mean} in the control treatment but were not in the E-CO_2 treatment. Therefore, averagely higher temperature regime during the flowering period could partially explain the E-CO_2-induced reduction in spikelet fertility of Nikomaru. In the E-Temp/E-CO_2 treatment, as compared with the E-temp treatment, difference in the T_{mean} was not significant. Furthermore, as compared with the E-temp treatment, T_{max} and T_{BH} in the E-Temp/E-CO_2 treatment were significantly low by 1.8 °C and 0.8 °C, respectively, due to accelerated heading, because the air temperatures in the control treatment during the calculation periods for T_{max} and T_{BH} in the E-Temp/E-CO_2 treatment were less than those in the control treatment during the periods in the E-Temp treatment. Therefore, further reduction in spikelet fertility than that in the E-Temp treatment by exposure to elevated CO_2 was not explained by the air temperature regime during the flowering period and before heading.

3.4 Stomatal conductance and canopy temperatures

Spikelet fertility decreases with increase in panicle temperature during flowering (Jagadish et al., 2007; Maruyama et al., 2013). Because elevated CO_2 induces stomatal closure (Ainsworth and Long, 2005; Hasegawa et al., 2016), exposure to elevated CO_2 reduces transpiration from leaves and increases canopy temperature (Bernacchi et al., 2007; Kimball, 2016; Long et al., 2006). In rice cultivated in the controlled environment chambers, Madan et al. (2012) reported the exposure to elevated CO_2 increased spikelet tissue temperature grown under relatively high air temperature conditions. Using FACE system in the paddy field, Yoshimoto et al. (2005) observed an elevated CO_2-induced reduction in stomatal conductance (g_s) in the leaves, which resulted in increased leaf and panicle temperatures. In this study, we measured g_s in the flag leaf immediately after and during the flowering periods of Nikomaru and Hinohikari, respectively. In both cultivars, the stomatal conductance in the flag leaf was significantly reduced by exposure to elevated CO_2 without any interaction (Fig. 3 and Table 2). Additionally, we detected significant increase in plant canopy temperature by both E-Temp and E-CO_2 treatments (Fig. 4). Increase in plant temperature by elevated air temperature was due to increase in air temperature (Table 1). Increase in plant temperature by elevated CO_2 could be due to reduced transpiration in the canopy via reduction in g_s (Fig. 3). Although the plant canopy temperature measured in this study does not exactly reflect the panicle temperature, increase in the temperature would reflect the increase in canopy temperature, including panicles, by both E-Temp and E-CO_2 treatments. Therefore, the reduction in spikelet fertility by both treatments could be due to increase in panicle temperature during the flowering period, in addition to high-temperature regime during this period due to changes in heading date in some cases.

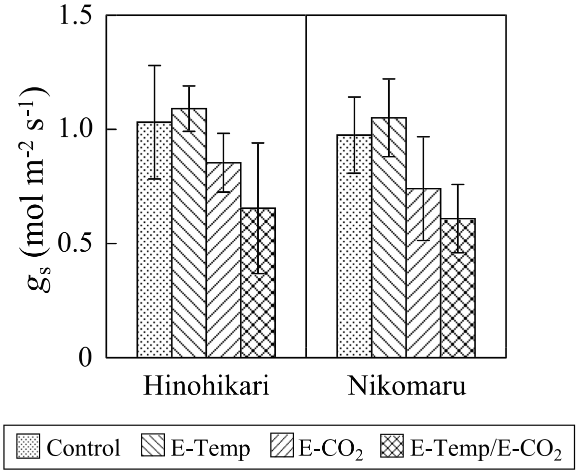

Fig. 3 Effects of elevated air temperature and elevated CO_2 on stomatal conductance (g_s) in flag leaves of two Japanese rice cultivars (*Oryza sativa* L., cvs. Hinohikari and Nikomaru) on 30 August 2019. Each value shows the mean of four chamber replications ($n = 4$), and each standard deviation is shown by a vertical bar. Three-way ANOVA results are shown in Table 2

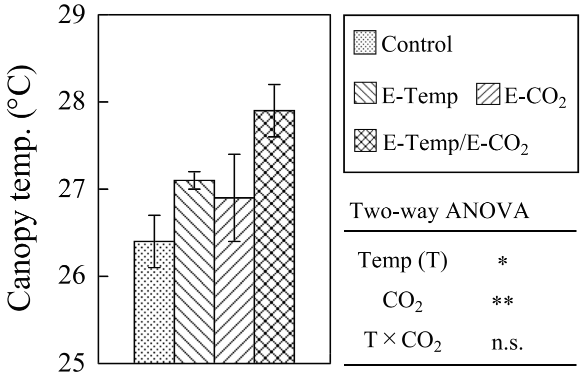

Fig. 4 Effects of elevated air temperature and elevated CO_2 on canopy temperature of rice (*Oryza sativa* L.) on 30 August 2019. Because the cultivars were mixed inside each chamber, the canopy temperature was determined for each chamber but not for each cultivar. Each value shows the mean of four chamber replications ($n = 4$), and each standard deviation is shown by a vertical bar. Two-way ANOVA: *$p < 0.05$, ** $p < 0.01$, n.s. = not significant

Compared with Hinohikari, Nikomaru is heat tolerant regarding grain quality (i.e., heat tolerant during grain filling period) (Tanaka et al., 2009; Tanamachi et al., 2016). In their report, the cultivar difference in the tolerance was reported using the cultivars cultivated under air temperature of 30 °C during grain filling stage after flowering. In the present study, the mean air temperature during the grain filling stage from flowering to the final harvest was lower than 30 °C in both cultivars. However, the hourly mean T_{air} exceeded 35 °C, above which the high-temperature injuries occur (Yoshida, 1981), 26 times during the period even if in the control treatment. Therefore, the reason why the elevated air temperature treatment caused the yield decrease not only in the heat-sensitive Hinohikari but also in the heat tolerant Nikomaru might be due to the high temperature in the control treatment. On the other hand, Maruyama et al. (2013) reported that there was no difference between the cultivars in heat tolerance regarding spikelet fertility (i.e., heat-tolerant trait during flowering period). This result was in accordance with the results of our present and previous studies (Yamaguchi et al., 2022). The characteristic traits in heat-tolerant cultivar regarding grain appearance quality are maintaining a nucellar epidermis and normal expression of starch-synthesis-related genes in the grains under high-temperature conditions (Tanamachi et al., 2016). On the other hand, Matsui et al. (2001) reported that high-temperature-induced floret sterility mainly due to the poor pollination and inhibition of the process after pollen germination. Therefore, the mechanisms underlying the heat tolerance regarding grain quality and spikelet fertility are different from each other, which could result in the no significant difference in the heat tolerance regarding spikelet fertility between the cultivars with different heat tolerance regarding grain appearance quality. To avoid the adverse effects of elevated air temperature and CO_2 on rice yield in the future, therefore, it is necessary to elucidate heat tolerance and develop a heat-tolerant cultivar regarding spikelet fertility because several researchers have reported cultivar difference in heat tolerance regarding spikelet fertility (Maruyama et al., 2013; Matsui et al., 2001).

In the control treatment, the spikelet fertility was not high (e.g., less than 60% of that in Nikomaru) (Table 3), and the air temperature was optimal or above optimal for the growth. Because elevated air temperature and elevated CO_2 additively affected spikelet fertility in both cultivars, we conclude that, under high-temperature conditions, elevated CO_2 exacerbated heat-induced spikelet fertility of the japonica rice cultivars Hinohikari and Nikomaru. Several researchers reported that elevated CO_2 exacerbated heat-induced reduction in spikelet fertility of the japonica rice cultivars "Koshihikari" and "Akihikari" and indica rice cultivar "IR72" by both chamber and FACE experiments (Kim et al., 1996; Kobayasi et al., 2019; Matsui et al., 1997). Hasegawa et al. (2016) and Cai et al. (2016) conducted FACE experiments and reported that elevated CO_2 reduced spikelet fertility of the japonica rice "Akitakomachi" and japonica hybrid rice "Changyou 5," respectively, in warm years. These results indicate that reduced spikelet fertility of rice by exposure to elevated CO_2 could be common under high-temperature conditions. Although this phenomenon could be explained by, in some cases, acceleration of heading, which results in a different air temperature regime including higher air temperature depending on the situation, the increase in panicle temperature via reduced transpiration in the canopy leaves during the flowering period could substantially cause elevated-CO_2-induced exacerbation of reduction in spikelet fertility under high-temperature conditions.

In the future, concurrent elevation of atmospheric CO_2 concentration and air temperature are projected (Canadell et al., 2021; Lee et al., 2021). In the region where heat stress on rice has become evident, rice yield could be less than that predicted by considering growth enhancement due to the elevated CO_2, because not only elevated air temperature but also elevated CO_2 significantly reduced spikelet fertility, and the combined effect was additive. Because the present study was conducted in one location in one particular year using chambers with two cultivars, further studies in another location with other cultivars grown under field condition are required to elucidate the growth and yield responses of rice to concurrent elevation of air temperature and atmospheric CO_2. However, the results obtained in the present study are useful information for considering rice yield under the conditions with elevated CO_2 and air temperature due to global warming, especially for regions where heat stress has become evident.

4 Conclusion

Elevated air temperature and elevated CO_2 significantly reduced grain yield of two japonica rice cultivars grown in a warm region where heat stress on rice has become evident. Among the yield components, reduction in spikelet fertility, the typical heat stress on rice, was the main cause of the yield reduction by both treatments in the two cultivars. The elevated CO_2-induced reduction in spikelet fertility could be caused by the higher temperature regime during the flowering period due to acceleration of heading, in some cases, and by increase in temperature of canopy, including panicles, via stomatal closure in canopy leaves. Because elevated air temperature and elevated CO_2 treatments additively reduced spikelet fertility, concurrent elevations of air temperature and CO_2 caused considerable reduction in grain yield in both cultivars.

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Authors' contributions
MY, conceptualization, methodology, formal analysis, investigation, data curation, and writing—original draft; NT, investigation and data curation; TN, methodology and data curation; TY, conceptualization and methodology; and TI, methodology and writing—review and editing. YK, conceptualization, supervision, and writing—review and editing.

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Availability of data and materials
The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests
The authors declare that they have no competing interests.

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