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To cite this article: Kazuhiro Kobayasi, Hidemitsu Sakai, Takeshi Tokida, Hirofumi Nakamura, Yasuhiro Usui, Mayumi Yoshimoto & Toshihiro Hasegawa (2019) Effects of free-air CO₂ enrichment on flower opening time in rice, Plant Production Science, 22:3, 367-373, DOI: 10.1080/1343943X.2019.1569472

To link to this article: <https://doi.org/10.1080/1343943X.2019.1569472>



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Published online: 04 Feb 2019.



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Effects of free-air CO₂ enrichment on flower opening time in rice

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ABSTRACT

Flower opening time (FOT) is important for reproductive success in higher plants. Rice plants exhibit phenotypic plasticity in FOT in response to environmental factors such as temperature. However, the effect of the concentration of atmospheric CO₂ ([CO₂]) on FOT has not yet been reported. Elevated [CO₂] (E-[CO₂]) increases the temperature of panicles, which may in turn advance FOT. We investigated the effect of E-[CO₂] on FOT in rice using a free-air CO₂ enrichment facility where we increased [CO₂] by about 200 μmol mol⁻¹ above the ambient level (A-[CO₂]). By photographing panicles at 10-min intervals, we determined 10%FOT and 50%FOT (the time of the day in Japan Standard Time when 10% and 50% of the flowers had opened, respectively). E-[CO₂] advanced 10%FOT and 50%FOT by 4 and 5 min at the 10% and 5% levels of significance, respectively. Daily mean air temperature (T_a), solar radiation, and vapor-pressure deficit were negatively correlated with 50%FOT. Regression line slopes for T_a versus 10%FOT and 50%FOT were slightly steeper for A-[CO₂] than those for E-[CO₂]. Our results suggest that the most probable reason why E-[CO₂] advanced FOT is an increase in panicle temperature arising from a reduction in leaf stomatal conductance.

Abbreviations: 10%FOT: the time of the day in Japan Standard Time when 10% of the flowers had opened; 50%FOT: the time of the day in Japan Standard Time when 50% of the flowers had opened; A-[CO₂]: ambient CO₂; [CO₂]: the concentration of atmospheric carbon dioxide; E-[CO₂]: elevated [CO₂]; FACE: free-air CO₂ enrichment; FOT: flower opening time; JST: Japan Standard Time; RH: relative humidity; Rs: solar radiation; T_a : air temperature; T_p : panicle temperature; VPD: vapor-pressure deficit

ARTICLE HISTORY

Received 9 September 2018
Revised 12 December 2018
Accepted 27 December 2018

KEYWORDS

Air temperature; elevated [CO₂]; flower opening time; free-air CO₂ enrichment; heat stress; rice

1. Introduction

The success of pollination or fertilization is largely determined by the flower opening time (FOT) in plants and angiosperms are evolved to optimize reproductive success at a minimal cost by optimizing their FOT (van Doorn & van Meeteren, 2003). Many plants open their flowers in the morning, but usually avoid doing so on mornings of very high humidity because dew encourages the growth of harmful fungi and bacteria (van Doorn & van Meeteren, 2003). In cultivated rice (*Oryza sativa* L.), FOT is adjusted according to the environment. In most indica rice, FOT occurs at around 10:00, whereas in most japonica rice, it occurs at around 11:00 in temperate zones such as Japan (Kobayasi et al., 2009).

FOT is affected by environmental factors such as air temperature (T_a), humidity, light intensity, and ratio of darkness to light (van Doorn & van Meeteren, 2003). Opening of flowers in many species, including rice, occurs in the morning, correlated with an increase in temperature and light intensity and with a decrease in

ambient humidity (van Doorn & van Meeteren, 2003). In rice, many meteorological factors, including T_a (Jagadish et al., 2007, 2008; Julia & Dingkuhn, 2012, 2013; Kobayasi et al., 2009; van Oort et al., 2014) and solar radiation (Kobayasi et al., 2010), affect FOT.

Rice plants exhibit phenotypic plasticity in FOT in response to environmental factors such as T_a , and therefore prediction of FOT is important when estimating the effects of heat-induced sterility in rice (Julia & Dingkuhn, 2012, 2013; Nguyen et al., 2014; van Oort et al., 2014) and also when evaluating the effectiveness of early-morning flowering cultivars, such as those developed by Ishimaru et al. (2010), Ishimaru et al. (2012), and Hirabayashi et al. (2015). By taking into account the transpirational cooling as well as FOT, van Oort et al. (2014) obtained a better estimation of fertility under heat stress conditions. Opening of flowers in rice plants in the early morning is a beneficial response to avoid sterility caused by heat stress at anthesis because the sensitivity of rice flowers to high temperatures

decreases during the 1-h period after flower opening (Satake & Yoshida, 1978; see also Bheemanahalli et al., 2017; Ishimaru et al., (2016); Kobayasi et al., 2010).

However, the effect of the concentration of atmospheric CO₂ ([CO₂]) on FOT is unclear, although an extreme concentration (>50000 μmol mol⁻¹) of CO₂ is known to trigger rice flower opening (Wang et al., 1989). Elevated [CO₂] (E-[CO₂]) increases the temperature of panicles (T_p) through the closing of stomata and reduction in leaf stomatal conductance (Oue et al., 2005; Shimono et al., 2010). Increased T_p caused by high [CO₂] may advance FOT, as it has been reported (Kobayasi et al., 2010) that higher T_a , higher solar radiation (R_s), and lower vapor-pressure deficit (VPD) in the early morning result in earlier FOT which together might affect FOT through their alteration of T_p . It is important to be able to assess and predict the effect of [CO₂] on FOT and heat stress on rice in order to evaluate the early-morning flowering cultivars under heat stress conditions combined with E-[CO₂].

In this experiment, we used the free-air CO₂ enrichment (FACE) facility at Tsukuba (Hasegawa et al., 2013). Rice plants grown under typical controlled environments, such as growth chambers, open their flowers 1–2 h later than those grown outdoors (Imaki et al., 1982). FACE is a more reliable platform as it eliminates such effects arising from the growth chamber and permits evaluation of the effect of [CO₂] on the physiological and ecological traits under open-field conditions (Kobayashi, 2001). Our objective in this experiment was to reveal the effect of E-[CO₂] on FOT in rice.

2. Materials and methods

2.1. Experimental site, plant material and culture methods

The study was conducted at the Tsukuba FACE site located in Ibaraki Prefecture, Japan (35°58'N, 139°60'E, 10 m above sea level) over a period of 6 years (2010–2015). We used a standard Japonica rice cultivar, 'Koshihikari'. The climate is humid subtropical with an average annual temperature of 13.8°C and annual precipitation of 1280 mm. Details of weather conditions and soil properties at the site are described by Hasegawa et al. (2013).

Crop cultivation practices in 2010 were reported by Hasegawa et al. (2013), and the 2011–2015 growing seasons followed essentially the same practices. Briefly, all plots received equal amounts of P and K in early April before ploughing, when the PK compound fertilizer was applied at a rate of 4.36 g m⁻² of P and 8.30 g m⁻² of K. The fields were kept submerged after late April. Three kinds of N fertilizer were applied just

prior to puddling: 2 g m⁻² as urea, 4 g m⁻² as one type of controlled-release fertilizer-coated urea (type LP100, JCAM Agri. Co. Ltd, Tokyo, Japan) and 2 g m⁻² as another type of controlled-release fertilizer (type LP140, JCAM Agri. Co. Ltd) in 2011, 2012, and 2013. In 2014, 2015, and 2016, LP140 was replaced with another controlled-release fertilizer (type LP40).

Seeds of the rice cultivar 'Koshihikari' were germinated in water and sown into seedling trays, each with 448 circular cells (16 mm in diameter and 25 mm in depth, Minoru Pot 448, Minoru Industrial Co. Ltd, Okayama, Japan). Each cell was filled with sterilized soil amended with fertilizer at the rate of 0.4 g N, 0.35 g P, and 0.5 g K per 1 kg of soil. Three seeds were sown in each cell. After seedling emergence, the seedling trays were transferred to the puddled open field and protected with a tunnel cloche or floating mulch for the first 2 weeks. The seedlings were manually transplanted into hills (three seedlings per hill) on May 26, May 25, May 23, May 22, May 22, and May 26 in 2010, 2011, 2012, 2013, 2014, and 2015, respectively. The planting density was 22.2 hills m⁻² (30 × 15 cm). After transplanting, the fields were kept flooded until August 20, ~3 weeks after heading, when the ponding water was drained for harvesting. We applied flush irrigations on several occasions to keep the soil moist.

2.2. CO₂ treatment

The method for controlling [CO₂] in an open field is described by Nakamura et al. (2012). Briefly, four blocks were established in paddy fields, with each block consisting of two octagonal plots (204 m², 17 m across): an ambient CO₂ (A-[CO₂]) plot and an E-[CO₂] treatment plot. The E-[CO₂] plots were equipped with emission tubes on the perimeter, where CO₂ was released from the windward side to keep the [CO₂] measured at the central point at about 200 μmol mol⁻¹ above the ambient control level.

Over the entire growing season (June–September), the mean A-[CO₂] at the site was 385, 379, 383, 384, 386, and 383 μmol mol⁻¹ in 2010, 2011, 2012, 2013, 2014, and 2015, respectively. The actual season-long mean [CO₂] in the FACE plots was 585, 560, 578, 576, 580, and 579 μmol mol⁻¹ in those years, respectively.

2.3. Measurement of FOT and weather

We measured FOT by taking photographs at 10-min intervals using a waterproof digital camera (WG-50, Ricoh, Tokyo, Japan), thus avoiding any physical stimuli of the panicles such as touching (Kobayasi et al., 2010). The photographs were recorded automatically in the

cameras. The details are described by Kobayasi et al. (2010). We defined 10%FOT and 50%FOT as the time of the day (Japan Standard Time; JST) when 10% and 50% of the flowers had opened on a given day, respectively. First, FOT were recorded on panicle basis. Subsequently, the mean of FOT among the measured panicles in each plot was determined.

We measured T_a , relative humidity (RH), wind speed, and R_s at the weather station of the Tsukuba FACE facility. A temperature and humidity sensor (HMP45D, Vaisala Inc., Helsinki, Finland) was installed 2 m above the soil surface with a forced-ventilated radiation shield. An anemometer and a wind vane (Model 03001-5 Wind Sentry, R. M. Young Co., Traverse City, MI, USA) were installed at a height of 2.5 m. Solar radiation was measured by using a pyranometer (LI-200SA, LI-COR Inc., Lincoln, NE, USA). The variables were measured every 10 s, and 10-min averages were recorded using a data logger (CR1000, Campbell Scientific Inc., Logan, UT, USA). VPDs were calculated from T_a and RH using the method of Buck (1981). T_a , RH, wind speed, and solar radiation are common in four replicates.

2.4. Statistics

We conducted an analysis of variance by applying a randomized block design, in which year, $[\text{CO}_2]$ treatment, and block are the factors, and year $\times [\text{CO}_2]$ is the interaction factor with four replications, using R (version 3.2.5, R Development Core Team 2016). We analyzed our data by means of correlation and multiple regression procedures using R. The FOT expressed as JST was converted into a value expressed as a decimal fraction when using statistical analyses. In all tests, statistical significance is indicated for $p < 0.001$, $p < 0.01$, or $p < 0.05$, and the actual p -values are presented where $0.05 < p < 0.1$.

3. Results

3.1. Weather during the flowering period

Daily mean T_a during the flowering period varied from 24.8°C to 29.2°C over a period of 6 years (Table 1). The daily mean

Table 1. Variations and means in daily mean, maximum, and minimum air temperatures (T_a , °C) during the flowering periods for 6 years.

Year	Daily mean T_a	Daily maximum T_a	Daily minimum T_a
2010	26.0–28.9 (28.0)	28.6–32.6 (31.6)	22.4–26.2 (25.0)
2011	22.3–27.0 (24.8)	24.0–31.6 (28.1)	20.6–24.4 (22.3)
2012	25.7–28.8 (27.2)	28.7–32.7 (31.3)	23.0–25.4 (23.6)
2013	22.9–27.7 (25.6)	26.7–32.2 (29.9)	20.4–24.2 (22.5)
2014	26.3–30.1 (28.4)	31.4–35.0 (33.4)	20.8–26.8 (23.9)
2015	28.6–29.6 (29.2)	33.9–35.1 (34.4)	23.5–24.9 (24.4)

Data are shown as maximum T_a –minimum T_a during the flowering periods (mean T_a averaged over the flowering periods).

T_a during the flowering period was highest in 2015 and in this year the daily maximum T_a sometimes reached 35°C, which is high enough for heat-induced floret sterility to occur. In contrast, the coolest year was 2011, with an average daily mean T_a of <25°C and daily minimum T_a not exceeding 25°C during the flowering period.

Daily mean wind speeds during the flowering period were light and never exceeded 3.2 m s⁻¹ (Table 2). The seasonal mean RH was lowest in 2014 (73.2%) and highest in 2013 (85.8%). The daily mean R_s in 2011 was lowest at 10.0 MJ m⁻² (when T_a was also the lowest) and that in 2014 was high at 23.6 MJ m⁻² (when T_a was relatively high).

3.2. Flower opening time

We detected significant differences in 10%FOT across years ($p < 0.001$) and $[\text{CO}_2]$ ($p = 0.052$), but the interaction was not significant (Table 3). E- $[\text{CO}_2]$ advanced 10%

Table 2. Variations and means in daily mean wind speed, relative humidity (RH), and daily solar radiation (R_s) during the flowering periods for 6 years.

Year	Daily mean wind speed (m s ⁻¹)	Daily mean RH (%)	Daily R_s (MJ m ⁻²)
2010	0.6–3.2 (2.2)	72.2–88.5 (79.0)	10.0–26.2 (19.8)
2011	0.2–1.3 (0.7)	83.2–88.3 (85.0)	4.0–13.9 (10.0)
2012	0.4–2.1 (1.1)	73.9–92.6 (82.0)	8.5–26.1 (21.1)
2013	0.7–1.9 (1.0)	77.1–92.9 (85.8)	12.2–25.6 (17.7)
2014	0.7–2.4 (1.4)	66.7–78.3 (73.2)	20.6–25.9 (23.6)
2015	0.7–1.7 (1.0)	75.1–79.7 (76.5)	21.4–26.4 (22.9)

Data are shown as maximum value–minimum value during the flowering periods (mean value averaged over the flowering periods).

Table 3. Effects of E- $[\text{CO}_2]$ on FOT and time span between 10%FOT and 50%FOT. 10%FOT and 50%FOT were the time when 10% and 50% of the flowers opened on a given day in Japan Standard Time (JST).

Year	Treatment	10% FOT	50% FOT	Time span between 10%FOT and 50%FOT (min)
2010	E- $[\text{CO}_2]$	10:05	10:21	16
	A- $[\text{CO}_2]$	10:01	10:21	20
2011	E- $[\text{CO}_2]$	10:20	10:52	32
	A- $[\text{CO}_2]$	10:36	11:01	25
2012	E- $[\text{CO}_2]$	10:09	10:45	36
	A- $[\text{CO}_2]$	10:12	10:50	38
2013	E- $[\text{CO}_2]$	10:34	10:53	19
	A- $[\text{CO}_2]$	10:40	10:59	18
2014	E- $[\text{CO}_2]$	10:19	10:35	16
	A- $[\text{CO}_2]$	10:21	10:41	20
2015	E- $[\text{CO}_2]$	10:02	10:19	17
	A- $[\text{CO}_2]$	10:05	10:22	17
Mean	E- $[\text{CO}_2]$	10:15	10:37	23
	A- $[\text{CO}_2]$	10:19	10:42	23
ANOVA	Year	***	***	***
	Treatment	0.052	*	ns
	Block	*	ns	**
	Year \times Treatment	ns	ns	ns

A- $[\text{CO}_2]$: ambient $[\text{CO}_2]$; E- $[\text{CO}_2]$: elevated $[\text{CO}_2]$; ns: not significant.

Statistically significant effects are indicated: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$. The value indicates the probability between 0.05 and 0.1.

FOT by 4 min on average. The 10%FOT in 2013 was the latest (when T_a was relatively low), while the 10%FOTs in 2010 and 2015 were the earliest (both years experiencing high daily mean T_a).

We also detected significant differences in 50%FOT across years ($p < 0.001$) and $[\text{CO}_2]$ ($p < 0.05$), but the interaction between year and $[\text{CO}_2]$ was not significant. E- $[\text{CO}_2]$ advanced 50%FOT by 5 min on average. The 50%FOT in 2011 was the latest, when T_a was the lowest. Time spans between 10%FOT and 50%FOT were different between years ($p < 0.001$), but $[\text{CO}_2]$ treatments and the interaction between year and $[\text{CO}_2]$ treatment showed no significant differences. In 2011 and 2012, the time spans between 10%FOT and 50%FOT were longer (about 30 min) than those in other years.

3.3. Relationship between FOT and weather factors

There were significant correlations between 10%FOT and daily mean T_a during the flowering period in both E- $[\text{CO}_2]$ and A- $[\text{CO}_2]$. The slope was a little steeper in A- $[\text{CO}_2]$ than that in E- $[\text{CO}_2]$; at lower daily mean T_a , the difference in 10%FOT between E- $[\text{CO}_2]$ and A- $[\text{CO}_2]$ was the greatest, reducing as daily mean T_a increased, with no difference as T_a approached 29°C where the regression lines intersect (Figure 1). Significant correlations between 50%FOT and daily mean T_a was also detected for both E- $[\text{CO}_2]$ and A- $[\text{CO}_2]$ (Figure 2).

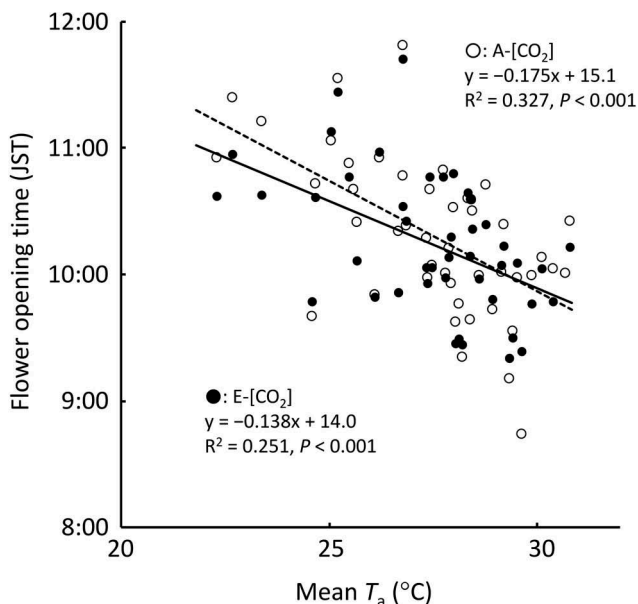


Figure 1. Relationship between 10%FOT (when 10% of the flowers open on a given day in JST) and mean air temperature (T_a) between 06:00 and 12:00 on each flowering day. Dotted line, A- $[\text{CO}_2]$; solid line, E- $[\text{CO}_2]$.

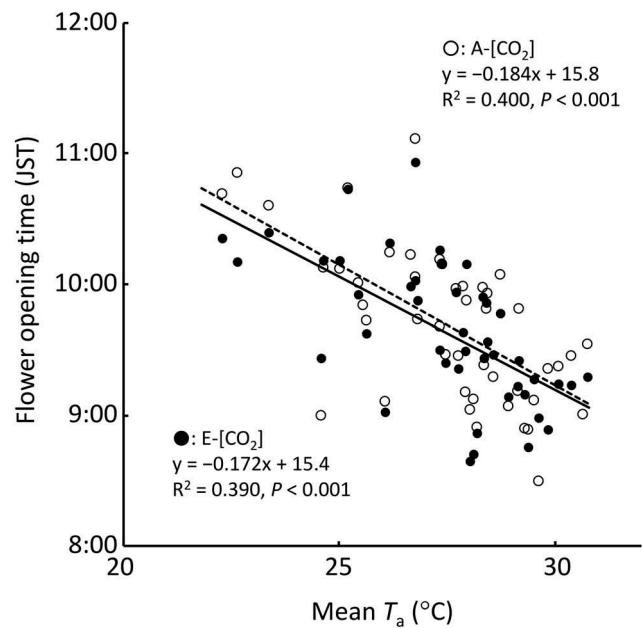


Figure 2. Relationship between 50%FOT (when 50% of the flowers open on a given day in JST) and mean air temperature (T_a) between 06:00 and 12:00 on each flowering day. Dotted line, A- $[\text{CO}_2]$; solid line, E- $[\text{CO}_2]$.

There was a significant correlation between 50%FOT and R_s during the flowering period in both E- $[\text{CO}_2]$ and A- $[\text{CO}_2]$ (Figure 3), with only a slight difference in the slopes of their regression lines. There was also a significant correlation between 50%FOT and VPD during the flowering

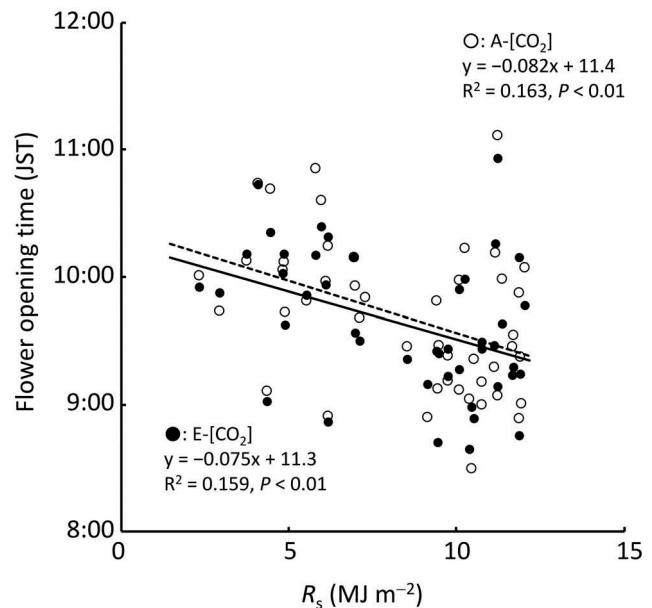


Figure 3. Relationship between 50%FOT (when 50% of the flowers open on a given day in JST) and solar radiation (R_s) between 06:00 and 12:00 on each flowering day. Dotted line, A- $[\text{CO}_2]$; solid line, E- $[\text{CO}_2]$.

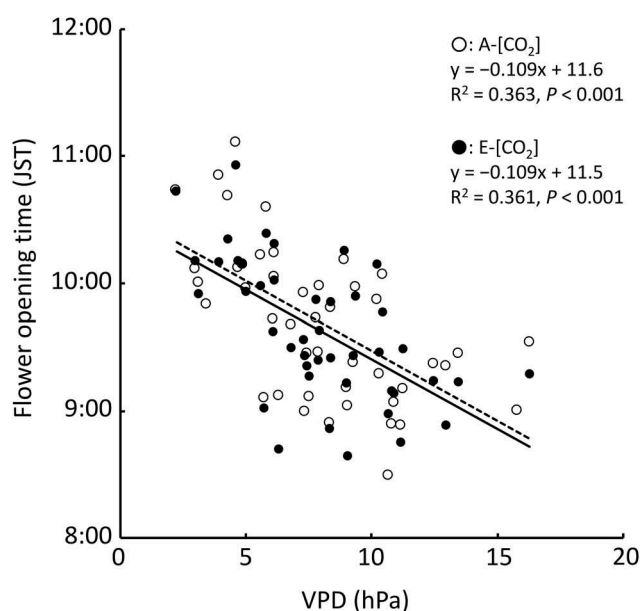


Figure 4. Relationship between 50%FOT (when 50% of the flowers open on a given day in JST) and mean VPD between 06:00 and 12:00 on each flowering day. Dotted line, A-[CO₂]; solid line, E-[CO₂].

period in both E-[CO₂] and A-[CO₂] (Figure 4), and their regression line slopes were almost identical.

4. Discussion

E-[CO₂] significantly advanced 10%FOT and 50%FOT by 4 and 5 min at the 10% and 5% levels of significance, respectively (Table 3). These results indicate that increasing [CO₂] by about 200 $\mu\text{mol mol}^{-1}$ in the open field advanced FOT, although the time difference between E-[CO₂] and A-[CO₂] was small. Many meteorological factors have been reported to affect FOT, including T_a (Jagadish et al., 2007, 2008; Julia & Dingkuhn, 2012, 2013; Kobayasi et al., 2010; van Oort et al., 2014), R_s (Kobayasi et al., 2010), VPD (Kobayasi et al., 2010), wind speed (Tsuboi, 1961), atmospheric pressure, and rainfall (Hoshikawa, 1989). In this experiment, we have demonstrated that [CO₂] is another meteorological factor affecting FOT.

The most probable reason why E-[CO₂] advanced FOT is an increase in T_p through a reduction in leaf stomatal conductance. Oue et al. (2005) observed that E-[CO₂] increased T_p at the FACE facility in China. Using a model simulation, Yoshimoto et al. (2005) estimated that the increase in T_p purely due to E-[CO₂] was 0.5–1.0°C on the day of flowering. Using a multiple regression model developed by Kobayasi et al. (2010), FOT advances by 15–30 min when T_a between 06:00 and 09:00 increases by 0.5–1.0°C. It is probable that the difference in T_a between E-[CO₂] and

A-[CO₂] during the preparation period for flower opening (06:00–09:00) is small. During the vegetative stage, stomatal conductance under E-[CO₂] at the Shizukuishi FACE was small at 09:00 and became larger around noon (Shimono et al., 2010). FOTs in our experiment were around 10:00–11:00, so the T_a difference just before starting of flower opening is likely to have been small and this would explain the small difference in FOT between E-[CO₂] and A-[CO₂]. The differences in the regression slopes between E-[CO₂] and A-[CO₂] also support this hypothesis (Figures 1 and 2), the slopes for A-[CO₂] being a little steeper than those for E-[CO₂]. In low-temperature conditions, the difference in FOT between E-[CO₂] and A-[CO₂] was larger; however, as the lower temperatures would lead to the rice flowers opening later, the difference in T_p would be greater and FOT would be advanced more.

The mechanism and organs involved in sensing heat or temperature that in turn determines FOT in rice have not been elucidated. Mittler et al. (2012) and Ruelland and Zachowski (2010) reviewed the methods by which plants sense heat or temperature: in sensing heat, calcium channels and membrane permeability play key roles. Tulip flower opening is a temperature-dependent process through water movement between petals and stems using water channels (Azad et al., 2004; van Doorn & Kamdee, 2014). In rice, expanding lodicules exert pressure on the lemma in flower opening (Hoshikawa, 1989). It is probable that calcium channels and water transport respond to heat or high temperature and move water or calcium between lodicules and outer organs, resulting in the expansion of the lodicules and opening of the rice flowers. Plant hormones are also linked with membrane fluidity and activation of ion channels (Mittler et al., 2012). Changes in microclimate affect physiology in plants, such as stomatal closure stimulated by plant hormones. For example, methyl jasmonate has been shown to play a role in signaling in guard cells and the closing of stomata (Jannat et al., 2012). Methyl jasmonate advances FOT (Kobayasi & Atsuta, 2010; Zeng et al., 1999). It is possible that plant hormones act to trigger flower opening as T_a increases.

VPD was negatively correlated with 50%FOT in this experiment (Figure 4) although Kobayasi et al. (2010) reported that higher T_a , higher R_s , and lower VPD in the early morning resulted in earlier FOT, using multiple-regression analysis. The correlation between daily mean T_a and VPD during the flowering period was high ($r = 0.826$; $p < 0.001$), so we tested multiple-regression analyses for 50%FOT with three covariates (T_a , R_s , and VPD during 06:00 and 09:00 in the flowering periods), using the data obtained in this experiment. However, the standardized partial regression coefficient of VPD was negative, which suggests that

a higher VPD would result in a later FOT. It is probable that humidity has two conflicting roles in determining flower opening: it affects FOT by influencing T_p , yet high humidity suppresses flower opening to reduce the likelihood of morning dew by enhancing the growth of harmful fungi and bacteria (van Doorn & van Meeteren, 2003). It might affect FOT through a balance of the two conflicting roles.

Although our experiment was conducted under subtropical conditions, rice plants receive stronger R_s in tropical conditions (between the Tropics of Cancer and Capricorn). In the tropics, stronger R_s might raise T_p when stomatal conductance is low due to E-[CO₂], when compared with subtropical conditions. To better assess and predict the effects of E-[CO₂] combined with the increased T_a on rice production and sterility, further experiments considering FOT are needed. Although future trends in [CO₂] are uncertain (depending mainly on human's endeavors to reduce fossil fuel consumption), it will be important to assess heat-induced floret sterility and advancement in FOT due to increase in T_p through E-[CO₂]. A micrometeorological model to simulate T_p (Yoshimoto et al., 2011) will also be helpful to predict FOT in E-[CO₂] in future rice production with considering the difference in the most sensitive time span between T_a and T_p in determining FOT.

Acknowledgments

The authors thank the students Mr. Sho Ushigaki, Mr. Kentaro Yamamoto, Mr. Wataru Hijikata, Ms. Sakiko Itano, Mr. Yuuki Nakagawa, Ms. Hitomi Hara, and Ms. Tomoko Adachi at Shimane University, Matsue, Japan. The authors would like to thank Enago (www.enago.jp) for the English language review.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported in part by the Ministry of Agriculture, Forestry and Fisheries, Japan, through a research project entitled 'Development of technologies for mitigation and adaptation to climate change in agriculture, forestry and fisheries', and in part by a Grant-in-Aid for Scientific Research on Innovative Areas [Grant number JP24114711] by the Japan Society for the Promotion of Science, as part of the project entitled 'Comprehensive studies of plant responses to high CO₂ world by an innovative consortium of ecologists and molecular biologists'.

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