

Original article

Effect of Elevated CO₂ and Temperature on Growth, Yield and Physiological Responses of Major Rice Cultivars by Region in South Korea

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Abstract The physiological characteristics, growth, and yield of each regional rice variety ('Odaebeo', 'Saechucheong', 'Ilmibeo') were investigated depending on the impact of changes in temperature and CO₂ concentration. Experiments were conducted with a control group, which reflected atmospheric CO₂ concentration and temperature, and treatment groups, in which the CO₂ concentration and temperature were increased by 250 ppm and 2.0°C from those in the control group. The results showed that the increase in CO₂ concentration and temperature reduced the growth and yield of the rice 'Odaebeo', but did not substantially change the productivity of the 'Saechucheong' and 'Ilmibeo'. The increase in CO₂ concentration and temperature increased stomatal conductance and rate of transpiration of the 'Odaebeo' variety, thereby decreasing its water use efficiency (WUE). In contrast, the increase in CO₂ concentration and temperature increased the photosynthetic rate and WUE of the 'Saechucheong' and 'Ilmibeo' varieties. The gradual change in climate is considered to directly affect growth and development of rice and diversely affect the productivity of each variety. Therefore, it is necessary to implement technological development, select regionally optimal rice varieties, develop new rice varieties, as well as conduct long-term monitoring of each rice variety for climate adaptation to counter global warming.

Key words: rice, yield, photosynthetic responses, production, climate change

INTRODUCTION

Climate change has had a discernible impact on the global production of several major crops. According to Pörtner *et al.* (2022), crop yield has declined in several countries, partly owing to rising temperatures and elevated CO₂ concentration.

Recent evidence indicates that climate-related risks to agriculture and food security in Asia will progressively escalate as global warming reaches 1.5°C and higher above pre-industrial levels (IPCC, 2018).

Rice (*Oryza sativa* L.) is one of the most important crops globally and the primary staple food in Asia, where approximately 90% of world's rice is produced and consumed; global rice consumption is projected to increase to approximately 490 million tons in 2020, and to around 650 million tons by 2050 (Rejesus *et al.*, 2012). Given the importance of rice, the

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effects of ongoing regional and global environmental changes on rice growth and yield need to be better understood. Thus, several studies have been conducted to examine the effects of elevated CO₂ level and temperature on rice growth and yield during the past few decades (Baker *et al.*, 1992; Madan *et al.*, 2012; Lee *et al.*, 2015a; Caine *et al.*, 2019; Chandio *et al.*, 2020).

The growth and yield of rice plants are markedly affected by increased CO₂ concentration and temperature (Conroy *et al.*, 1994; Cheng *et al.*, 2009; Kimball *et al.*, 2016; Wang *et al.*, 2020). Rice responses to climate change vary with region and rice cultivars. Additional research confirmed that climate change will disproportionately affect crop yields among regions, with more negative than positive effects being expected in most areas, especially in currently warm regions, including Africa and Central and South America (Pörtner *et al.*, 2022). In addition, crop yields could increase by up to 20% in East and South-East Asia, but could decrease by up to 30% in Central and South Asia by the mid-21st century (IPCC, 2014). Moderate warming benefits cereal crop and pasture yields in the mid- to high-latitude regions, but even slight warming decreases yields in seasonally dry and tropical regions. Although agriculture is known to be highly dependent on climate, little evidence of observed changes related to regional climate changes has been noted.

Hence, there is a need for more experiments on various cultivars of rice under global warming situation in many areas, and intraspecific variation could be used to select for optimal cultivars, which would maximize commercial productivity in a high CO₂ concentration and temperature environment. On average, adaptations such as changing varieties and planting times can prevent a 10~15% reduction in yield under a 1~2°C increase in local temperature (IPCC, 2014). Thus, identifying and developing cultivars that respond well to elevated CO₂ level can be an important option for adaptation to climate change (Ziska *et al.*, 2012).

Research on creating models for predicting changes in the growth and productivity of rice according to climate change,

simulation methods, and their use in vulnerability evaluation of rice productivity has been conducted in Korea (Shim *et al.*, 2010; Kim *et al.*, 2013; Seo *et al.*, 2020). but there is lack of experimental research on changes in growth and productivity of rice according to elevated CO₂ concentration and temperature. Recently, partial research on properties of change in growth and productivity of rice seedlings under global warming environment was conducted (Lee *et al.*, 2015b; Oh *et al.*, 2018). However, only one factor, either temperature or CO₂ concentration, was considered in the experiment. Thus, realistic experimental data are required for accurate prediction of the changes in rice yield depending on future climate change and for developing adequate countermeasures.

The purpose of this study was to provide basic data for selecting cultivars that can adapt well to climate change. Suitable cultivars for cultivation in response to future climate change were selected based on the effects of increased CO₂ concentration and temperature on the physiological properties, yield, and growth of three main rice cultivars per region.

MATERIALS AND METHODS

1. Plant cultivars

The rice cultivar that has the largest cultivation area in the region was selected for this study: ‘Odaebyeo’ (Early maturing rice) in the northern region, ‘Saechucheong’ (Mid-late maturing rice) in the central region, and ‘Ilmibyeo’ (Mid-late maturing rice) in the southern region. The seedlings were obtained from the National Institute of Crop Science. A description of the individual cultivars used is given in Table 1.

2. Experimental design

This study was conducted in glass greenhouse (12 m × 7.8 m × 5 m). The surface area of the control and treatment groups was 46.8 m², respectively. The control group maintained atmospheric CO₂ concentration and temperature. The

Table 1. General description of the rice cultivars used in this experiment.

Cultivar	Cultivation areas	Maturity	Seeding period	Transplanting period	Heading period
Odaebyeo	Central and Northern	Early	4/15~25	5/20~25	7/26
Saechucheong	Central and Southern	Medium-late	4/25	5/25	8/19
Ilmibyeo	Southern	Medium-late	4/25	5/25	8/19

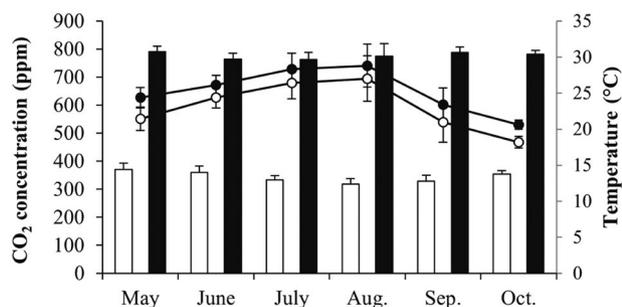


Fig. 1. Monthly mean CO₂ concentration and temperature in the control (open symbols) and treatment (closed symbols) groups throughout the experimental period in 2012. Vertical bars denote \pm SE of the mean.

treatment group had higher CO₂ concentration and temperature than the control group by +429.4 ppm and 2.0°C (Fig. 1). CO₂ gas tank connected to a gas regulator with a hose (2.0 mm in diameter) was installed in the treatment group, and the gas was released from the ceiling of the greenhouse, considering that CO₂ is heavier than air. In addition, ventilating fans were installed for air circulation. CO₂ concentration was controlled with an LCSEMS Automatic Sensor (LCSEMS-002, Parus Co., Korea) linked to a computer to set the desired concentration range. It was programmed so that gas valve closes if the level of CO₂ concentration in the treatment group exceeds the programmed range. CO₂ concentration, temperature, and relative humidity were measured and monitored in 10 min intervals using the automatic sensor.

3. Cultivation and harvesting

The rice seeds used in the study were selected through salt solution selection process (specific gravity 1.13) before they were sown to screen high quality seeds. Then, the seeds were disinfected by using the hot water disinfection method, in which the seeds were immersed under warm water at 60°C for 10 min. The hot water disinfection method is an effective method that disinfects the seeds with high temperature and it helps maintain a stable germination rate of rice seeds. The disinfected seeds were soaked in water for 3~4 days at room temperature so that it could sprout equally.

In 2012 April~May, four sprouts were directly planted at equal intervals in each Wagner pots, and this was repeated five times for each cultivar. The fertilizers were used at a level of N - P₂O₅ - K₂O = 13 - 5.1 - 7.1 g m⁻².

Nitrogen as a pre-planting fertilizer, topdressing at the tiller-

ing stage, fertilizer at the panicle initiation stage, and top-dressing at the ripening stage was used at a ratio of 50 : 20 : 20 : 10. Kali (potassium carbonate) as a pre-planting fertilizer and fertilizer at the panicle initiation stage was used at a ratio of 70 : 30, and phosphorous was used as a pre-planting fertilizer. The water depth was maintained at 3~5 cm at all times.

The soil used in the experiment was collected from rice paddy wetlands around the Geum River Basin. The plants were directly planted in Wagner pots. They were cultivated in each of the control and treatment groups. The cultivation period was from April to October 2012, and the plants were harvested in October.

4. Growth and yield determination

In October 2012, 120 individuals were harvested from each pot to determine growth and yield. Plant height was measured, and the number of leaves, tillers, and panicles were counted. Next, all plant parts of each hill were separated into leaf blades, stems (including leaf sheaths and culms), and roots.

To determine grain yield and its components, panicle number per tiller and panicle length were measured, and the grains were carefully threshed. Then, the number of total and filled grains per panicle was counted. Percentage of filled grains was referred to as the percentage of unfilled grains number to total grains. After air-drying for 2 weeks, the dry weight of leaves, stems, root, panicles, and grains were measured. Total plant biomass was obtained separately from the roots, and included the leaves, stems, and panicles for green and senesced materials. The harvest index (HI) was then calculated as the ratio of grain yield to total plant biomass.

5. Gas-exchanged measurements

Photosynthetic rate, transpiration rate, and stomatal conductance per unit area of leaf were measured by using a portable photosynthesis analyzer and a 6.25 cm² chamber for broadleaf trees on a clear day in July 2012 between 10:00 A.M. and 2:00 P.M. to investigate the photosynthetic response of the three rice cultivars to increases in CO₂ concentration and temperature.

6. Leaf C : N ratio, nitrogen content, and carbon content

Leaf, stem, grain, and root samples were dried for 2 days at

65°C and then pulverized into a fine powder using a blender (AKM-369s; Eupa, Seoul, Korea). Nitrogen and carbon concentrations were determined using an automatic elemental analyzer (Flash EA 1112 series; Thermo Fisher Scientific, Rochester, NY, USA) at the Center for Research Facilities, Chungnam National University. The C:N ratio was calculated as the ratio of carbon content to nitrogen content.

7. Statistical analysis

The effects of elevated CO₂ and temperature on the growth, yield, and physiological parameters of three rice cultivars were confirmed via one-way ANOVA, and the statistical differences between the control and treatment groups were evaluated by Fisher's least significant difference *post-hoc* test, with significance set at $P=0.05$. Multivariate analysis of variance (MANOVA) was used to analyze the effects of elevated CO₂ concentration and temperature, cultivars, and their interaction within each species. All statistical analyses were

performed at a 0.05 confidence level using the STATISTICA 8 software (Statsoft, Inc., Tulsa, OK, USA).

RESULTS AND DISCUSSION

1. Growth and yield

The growth and quantitative responses of three rice cultivars to elevated CO₂ concentration and temperature are shown in Tables 2, 3.

The height of the aboveground part of 'Odaebyeo' was higher by 106.02 ± 5.41 cm plant⁻¹ in the treatment group than in the control group, but leaf number, tiller number, and stem weight were lower in the treatment group than in the control group by 3.45 ± 1.36 ea plant⁻¹, 15.15 ± 4.77 ea plant⁻¹, and 2.81 ± 0.61 g plant⁻¹, respectively (Table 2). In addition, the aboveground biomass of 'Odaebyeo' was higher in the control group (6.59 ± 1.22 g plant⁻¹) than in the treatment group

Table 2. Vegetative growth responses of three rice cultivars under the control (ambient CO₂ and temperature) and treatment (elevated CO₂ and temperature).

Parameters	Odaebyeo		Saechucheong		Ilmibyeo	
	Control	Treatment	Control	Treatment	Control	Treatment
Plant height (cm plant ⁻¹)	100.81 ± 7.61	106.02 ± 8.27*	106.72 ± 5.41	104.90 ± 7.97	101.42 ± 5.03	102.64 ± 9.29
No. of leaves (ea plant ⁻¹)	4.75 ± 1.65*	3.45 ± 1.36	19.05 ± 6.44	28.50 ± 10.07*	28.20 ± 12.85	26.00 ± 12.91
No. of tillers (ea plant ⁻¹)	18.20 ± 3.66*	15.15 ± 4.77	2.37 ± 0.68	3.05 ± 1.28*	3.75 ± 3.31	4.37 ± 3.82
Leaf weight (g plant ⁻¹)	1.31 ± 0.24	1.36 ± 0.40	1.54 ± 0.42	2.20 ± 0.96*	2.14 ± 1.00	2.10 ± 1.38
Stem weight (g plant ⁻¹)	2.81 ± 0.61*	2.35 ± 0.59	2.68 ± 0.85	4.24 ± 2.62*	3.75 ± 1.90	3.46 ± 2.54
Aboveground biomass (g plant ⁻¹)	6.59 ± 1.22*	5.58 ± 1.54	6.98 ± 2.41	9.93 ± 4.87*	10.00 ± 5.39	9.76 ± 6.64
Belowground biomass (g plant ⁻¹)	1.35 ± 0.31	1.48 ± 0.54	1.15 ± 0.83	1.67 ± 1.06	1.59 ± 1.06	1.39 ± 1.34
Total biomass (g plant ⁻¹)	7.94 ± 1.35	7.06 ± 2.05	8.13 ± 3.14	11.60 ± 5.79*	11.59 ± 6.33	11.15 ± 67.79
RSR (mg g ⁻¹)	209.01 ± 47.98*	261.71 ± 38.45	154.76 ± 65.43	162.36 ± 62.15	153.80 ± 56.89	137.50 ± 63.13

The data are shown as means and standard errors.

* indicates significant differences between control and treatment (Fisher's least significant difference, $P < 0.05$).

($5.58 \pm 1.54 \text{ g plant}^{-1}$) under elevated CO_2 concentration and temperature conditions.

The leaf weight, belowground biomass, and plant biomass did not differ considerably in gradient, but RSR was higher in the treatment group with elevated CO_2 concentration and temperature.

‘Saechucheong’, the most cultivated rice cultivar in the central region, had higher number of leaves (+49.6%), number of tillers (+28.7%), leaf weight (42.9%), stem weight (+58.2%), aboveground biomass (+42.3%), and plant biomass (+42.7%) in the treatment group than in the control group under elevated CO_2 concentration and temperature conditions. Plant height, belowground biomass, and RSR were not much different in gradient. In the case of ‘Ilmibyeo’, no statistical differences were detected between the control and treatment groups in all growth fields (Table 2).

The yield change of three rice cultivars caused by elevated CO_2 concentration and temperature is shown in Table 3. The total panicle weight, total grain weight, and HI of ‘Odaebyeo’ in the control group were $2.47 \pm 0.66 \text{ g plant}^{-1}$, $2.19 \pm 0.65 \text{ g plant}^{-1}$, and $0.33 \pm 0.07 \text{ g plant}^{-1}$, respectively, which were higher than those in the treatment group. However, ‘Saechucheong’ showed no differences between the control and treatment groups in every section, except for the total weight

of empty seeds. In the case of ‘Ilmibyeo’, the total grain number and grain weight were higher in the treatment group by 3.4% and 23.3%, respectively, than in the control group.

Shim *et al.* (2010) predicted that the national average rice harvest will decrease by 4.5~8.2% in the case of a 2~3°C increase in the average temperature from the 30-year average climate (1971~2000). Shang *et al.* (2018) cultivated rice in a Soil Plant Atmosphere. Research (SPAR) System under increased temperature (+2.8°C) and CO_2 concentration (+580 ppm) from the atmospheric environmental conditions. As a result, the growth period was curtailed as the heading date advanced by 5 days or above compared to the current date, and the risk to exposure to high-temperature ripening increased. Therefore, a substantial reduction in the yield and quality of future rice production was predicted.

The HI represents the rate of grain yield to the total dry weight of the rice plant, and the total dry weight and HI must be high for high rice yield. In the present study, the aboveground biomass and HI of the rice ‘Odaebyeo’ decreased under high temperature and CO_2 concentration conditions. This implies that the yield of rice that directly relates to productivity was reduced. In contrast, the ‘Saechucheong’ rice variety was not affected by changes in temperature and CO_2 concentration, and the yield of ‘Ilmibyeo’ rice variety

Table 3. Yield components of three rice cultivars under control (ambient CO_2 and temperature) and treatment (elevated CO_2 and temperature).

Parameters	Odaebyeo		Saechucheong		Ilmibyeo	
	Control	Treatment	Control	Treatment	Control	Treatment
Total panicle weight (g plant ⁻¹)	2.47 ± 0.66*	2.00 ± 0.78	2.75 ± 1.28	3.49 ± 1.40	4.11 ± 2.54	4.20 ± 2.86
No. of total grains (ea plant ⁻¹)	76.50 ± 20.69	65.90 ± 25.12	120.53 ± 52.57	137.80 ± 50.31	161.15 ± 27.10	166.63 ± 35.91*
Total grains weight (g plant ⁻¹)	2.19 ± 0.65*	1.76 ± 0.67	2.62 ± 1.22	3.14 ± 1.21	3.18 ± 1.33	3.92 ± 1.69*
No. of total unfilled grains (ea plant ⁻¹)	29.25 ± 15.51	31.25 ± 15.34	28.00 ± 7.14	31.10 ± 8.63	30.20 ± 15.60	22.95 ± 9.70
Total unfilled grains weight (g plant ⁻¹)	0.16 ± 0.12	0.16 ± 0.08	0.08 ± 0.04	0.14 ± 0.09*	0.12 ± 0.09	0.08 ± 0.07
Grain filling ratio (%)	73.34 ± 10.01	69.13 ± 9.03	79.95 ± 5.51	82.92 ± 8.62	82.56 ± 7.75	85.33 ± 9.25
Harvest index	0.33 ± 0.07*	0.29 ± 0.07	0.36 ± 0.07	0.33 ± 5.51	0.35 ± 0.05	0.38 ± 0.07

The data are shown as means and standard errors.

* indicates significant differences between control and treatment (Fisher’s least significant difference, $P < 0.05$).

increased.

In a previous study, eight rice varieties were cultivated under identical methods and high-temperature conditions; the results showed significant differences among the varieties. In particular, the rice ‘Odaebyeo’ reacted most sensitively to the temperature conditions, and the yield of rice decreased as temperature increased (Lee *et al.*, 2015a). This was identical to the results of our study.

Lee *et al.* (2011) found that the growth temperature elevated and growing period curtailed as global warming accelerated, and they were concerned that the quality and yield of rice would degrade. In particular, their prediction that only the species with substantial growth period curtailment would suffer damage was distinct from the result of the present study. The late-harvested ‘Ilmibyeo’ rice variety, with the longest growth period, did not undergo changes in growth and development, but its yield was increased compared to the other two varieties.

Ziska *et al.* (1996) comparatively analyzed the intraspecific variations for 17 varieties according to increases in temperature and CO₂ concentration. The response in growth and change in yield of rice differed for each variety. The species-specific characteristics vary, so intraspecific variation may diversify according to environmental change. Therefore, it is

necessary to study the growth and reproduction of various species under future climatic conditions. Accumulated response data for each rice variety could significantly improve the selection of the varieties with the optimal productivity under future warmer climates.

In particular, the study of species that respond sensitively to environmental change needs to be prioritized. In addition, in-depth research is required on forecasting the productivity of rice varieties mainly cultivated in the northern regions of South Korea, such as the rice ‘Odaebyeo’.

2. Photosynthetic responses

Changes in the photosynthetic characteristics of three rice cultivars according to elevated CO₂ concentration and temperature are shown in Figs. 2~4.

The photosynthetic rate of ‘Odaebyeo’ in the treatment group with high CO₂ concentration and temperature did not show marked difference compared to the control group, but transpiration rate ($5.14 \pm 0.90 \text{ mmol m}^{-2} \text{ s}^{-1}$) and stomatal conductance ($0.31 \pm 0.08 \text{ mmol m}^{-2} \text{ s}^{-1}$) were higher in the treatment group than in the control group, whereas water use efficiency ($1.98 \pm 0.32 \text{ } \mu\text{mol CO}_2/\text{mmol H}_2\text{O}$) was lower (Fig. 2).

The photosynthetic rate of ‘Saechucheong’ was higher in

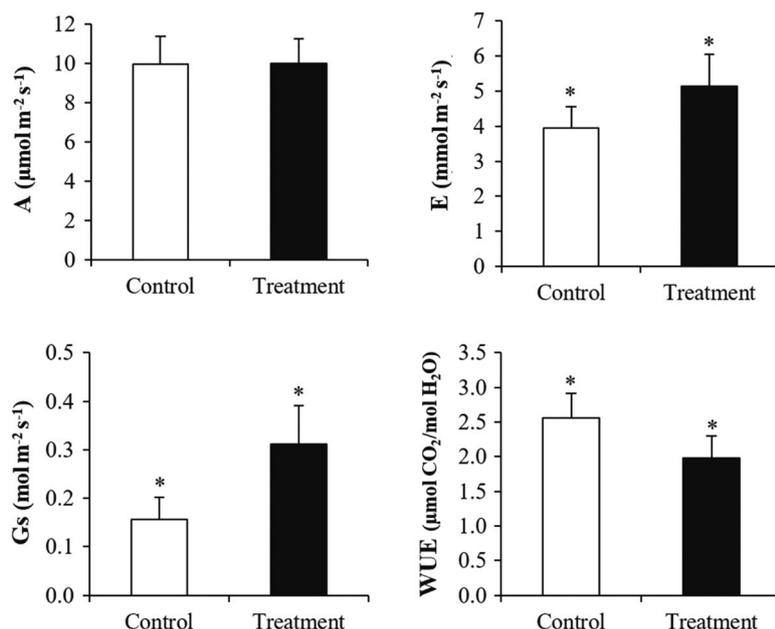


Fig. 2. Photosynthetic rate (A), transpiration rate (E), stomatal conductance (Gs), and water use efficiency (WUE) of rice ‘Odaebyeo’ grown under control and treatment conditions. * signs on the bars indicate significant differences between control (ambient CO₂ and temperature) and treatment (elevated CO₂ and temperature) (Fisher’s least significant difference, $P < 0.05$).

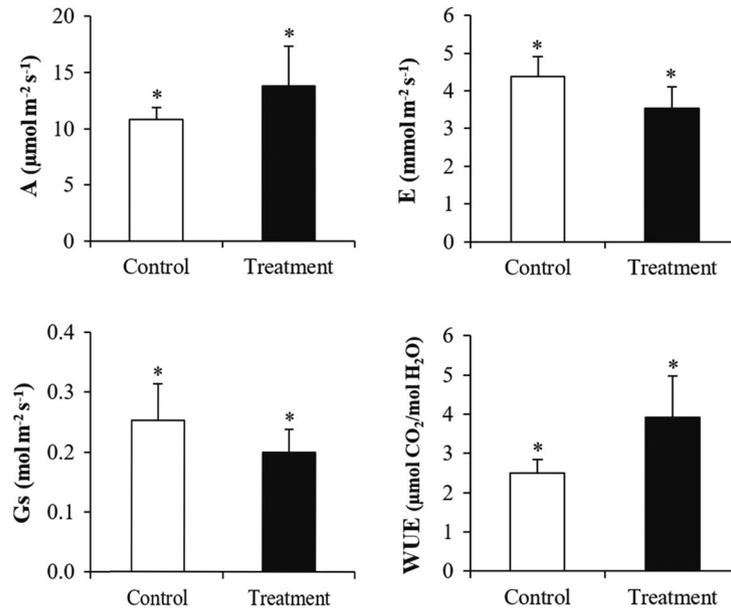


Fig. 3. Photosynthetic rate (A), transpiration rate (E), stomatal conductance (Gs), and water use efficiency (WUE) of rice 'Saechucheong' grown under control and treatment conditions. * signs on the bars indicate significant differences between control (ambient CO_2 and temperature) and treatment (elevated CO_2 and temperature) (Fisher's least significant difference, $P < 0.05$).

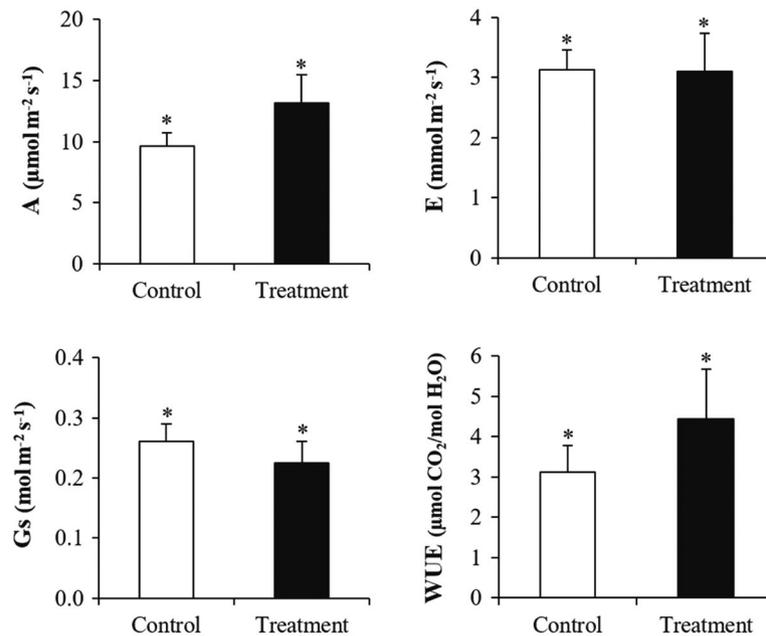


Fig. 4. Photosynthetic rate (A), transpiration rate (E), stomatal conductance (Gs), and water use efficiency (WUE) of rice 'Ilmibyeo' grown under control and treatment conditions. * signs on the bars indicate significant differences between control (ambient CO_2 and temperature) and treatment (elevated CO_2 and temperature) (Fisher's least significant difference, $P < 0.05$).

the treatment group ($13.77 \pm 3.58 \mu\text{mol m}^{-2} \text{s}^{-1}$) than in the control group ($10.82 \pm 1.04 \mu\text{mol m}^{-2} \text{s}^{-1}$). Water use efficiency was also higher in the treatment group ($3.92 \pm 1.04 \mu\text{mol CO}_2/$

$\text{mmol H}_2\text{O}$) than in the control group ($2.50 \pm 0.34 \mu\text{mol CO}_2/\text{mmol H}_2\text{O}$). In contrast, the transpiration rate and stomatal conductance of 'Saechucheong' were $3.55 \pm 0.56 \text{mmol m}^{-2}$

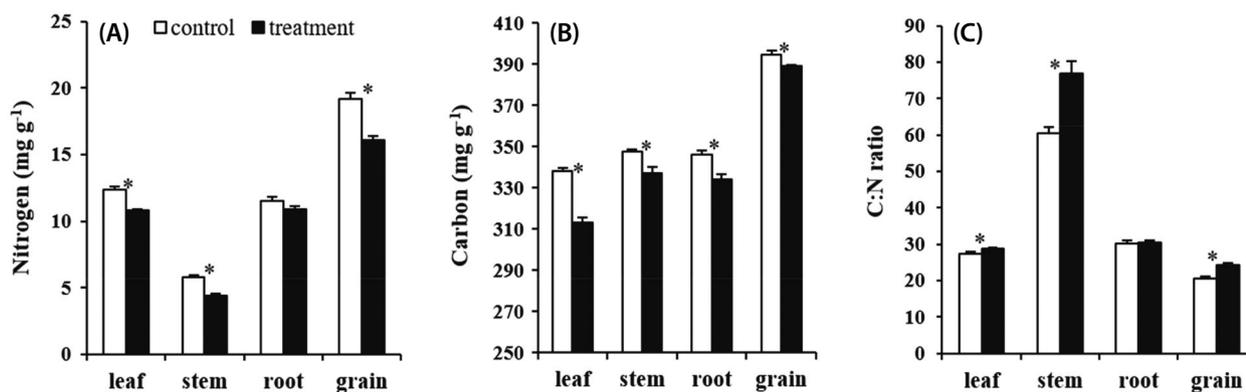


Fig. 5. Nitrogen (A), carbon (B), and C : N ratio (C) of rice ‘Odaebyeo’ grown under control (ambient CO₂ and temperature) and treatment (elevated CO₂ and temperature) conditions. * signs on the bars indicate significant differences in each organ between control and treatment (Fisher’s least significant difference, $P < 0.05$).

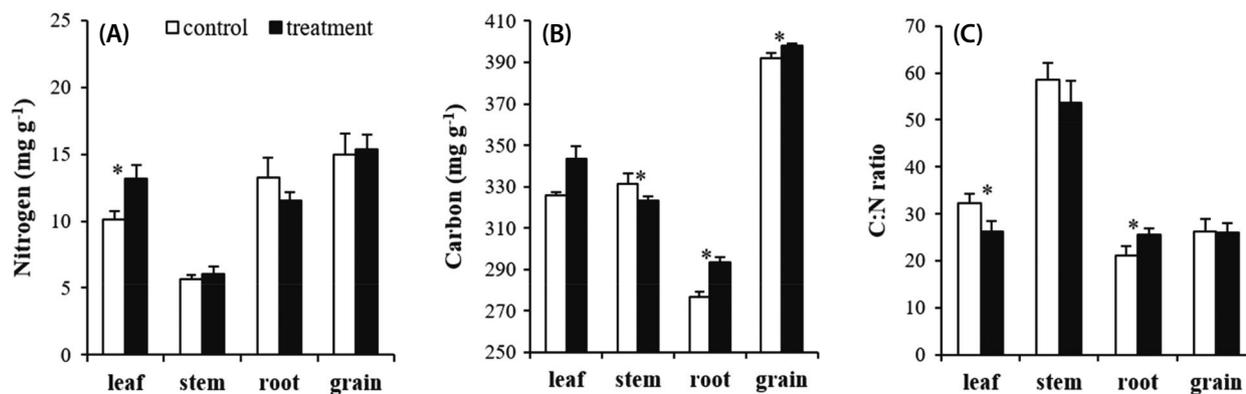


Fig. 6. Nitrogen (A), carbon (B), and C : N ratio (C) of rice ‘Saechucheong’ grown under control (ambient CO₂ and temperature) and treatment (elevated CO₂ and temperature) conditions. * signs on the bars indicate significant differences in each organ between control and treatment (Fisher’s least significant difference, $P < 0.05$).

s⁻¹ and $0.20 \pm 0.04 \text{ mmol m}^{-2} \text{ s}^{-1}$, respectively, under elevated CO₂ concentration and temperature conditions, which were lower than those in the control group (Fig. 3).

The photosynthetic rate and water use efficiency of ‘Ilmi-byeo’ grown in the treatment group, under elevated CO₂ concentration and temperature conditions, were $13.15 \pm 2.29 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and $4.43 \pm 1.25 \mu\text{mol CO}_2/\text{mmol H}_2\text{O}$, respectively, which were higher than those in the control group. However, stomatal conductance was lower in the treatment group ($0.22 \pm 0.04 \text{ mol m}^{-2} \text{ s}^{-1}$) than in the control group ($0.26 \pm 0.03 \text{ mol m}^{-2} \text{ s}^{-1}$), and no difference was observed in the transpiration rate between gradients (Fig. 4).

Changes in the nitrogen content, carbon content, and C : N ratio in the organs (leaf, stem, root, grain) of three rice cultivars under elevated CO₂ concentration and temperature condi-

tions are described in Figs. 5~7. The nitrogen content in the leaf, stem, and grain of ‘Odaebyeo’ in the treatment group, with elevated CO₂ concentration and temperature, was lower than that in the control group (Fig. 5A). Carbon content per organ was lower in the treatment group than in the control group (Fig. 5B). The C : N ratio of the leaf, stem, and grain of ‘Odaebyeo’ was higher in the treatment group than in the control group (Fig. 5C).

In the case of ‘Saechucheong’, leaf nitrogen content was higher in the treatment group ($13.15 \pm 1.00 \text{ mg g}^{-1}$) than in the control group ($10.10 \pm 0.61 \text{ mg g}^{-1}$). However, there were no differences in the nitrogen content of the stem, root, and grain between gradients (Fig. 6A). Leaf, root, and grain carbon content was higher in the treatment group than in the control group, but there was no difference in stem carbon content

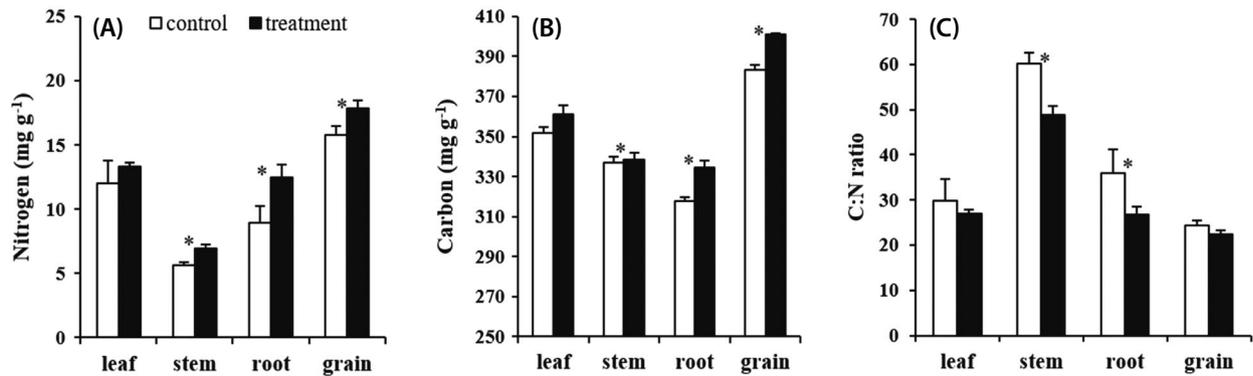


Fig. 7. Nitrogen (A), carbon (B), and C:N ratio (C) of rice ‘Ilmibyeo’ grown under control (ambient CO₂ and temperature) and treatment (elevated CO₂ and temperature) conditions. * signs on the bars indicate significant differences in each organ between control and treatment (Fisher’s least significant difference, $P < 0.05$).

between gradients (Fig. 6B). The leaf C:N ratio of ‘Saechucheong’ was lower in the treatment group (26.24 ± 2.30) than in the control group (32.31 ± 1.93), but the root C:N ratio was higher in the treatment group (25.46 ± 1.51) than in the control group (21.05 ± 2.06) (Fig. 6C). The nitrogen content in the stem, root, and grain of ‘Ilmibyeo’ in the treatment group increased by 23.7%, 39.7%, and 13.05%, respectively, compared with those in the control group (Fig. 7A). Furthermore, the carbon content increased to a greater degree in the treatment group (leaf, $360.90 \pm 4.50 \text{ mg g}^{-1}$; root, $334.49 \pm 3.40 \text{ mg g}^{-1}$; grain, $401.09 \pm 0.61 \text{ mg g}^{-1}$) than in the control group (Fig. 7B). The stem and root C:N ratios of ‘Ilmibyeo’ were decreased to a greater degree in the treatment group than in the control group, but there were no differences between gradients for the leaves and grain (Fig. 7C).

In general, CO₂ concentration and temperature directly affect the photosynthetic capacity of plants, and their impacts on rice cultivation have long been studied (Lin *et al.*, 1997; Sakai *et al.*, 2001; Wang *et al.*, 2020). However, there is a lack of studies on a variety of species under identical environmental conditions. In the present study, each rice variety responded distinctly to climate change in terms of physiology, growth, and yield.

The rice ‘Odaebyeo’ photosynthetically responded more sensitively to environmental change than the other two varieties. The transpiration rate and stomatal conductance increased owing to increases in CO₂ concentration and temperature, and the WUE decreased accordingly. These changes directly affected the growth and yield of the ‘Odae byeo’. The concomitant increases in temperature and CO₂ concentration degraded the photosynthetic capacity and WUE of the rice ‘Odaebyeo’

and reduced the rice harvest productivity. In contrast, the WUE of ‘Saechucheong’ and ‘Ilmibyeo’ rice varieties increased under high CO₂ concentration and temperature conditions.

Elevated CO₂ concentrations reduce stomatal apertures of the leaves and reduce transpiration (Morison, 1998), but high temperatures may offset this effect and decrease the WUE. For this reason, the development of varieties that have optimal WUE even under warm climatic conditions in the future has been investigated by modification of genes that regulate the density or size of the stomata (Bertolino *et al.*, 2019; Dunn *et al.*, 2019). The present study verified that each rice ecotype responds diversely to change in environmental factors. In the future, long-term monitoring of the growth, yield, and physiological characteristics of the widely cultivated rice species and other genetically modified varieties will be necessary.

CONCLUSION

This study investigated the impact of CO₂ and temperature increases on the growth and yield of rice and provides preliminary data for fostering and selecting rice varieties that are adapted to changes in climate and cultivating land. The results showed that CO₂ concentration and temperature increases affected the growth and yield of rice, and the response differed for each ecotype. The growth and yield of the rice ‘Odaebyeo’, unlike the other two varieties, responded negatively to increases in CO₂ concentration and temperature, and its productivity is predicted to decrease in the future.

The results of crop growth simulation of spatiotemporal changes in rice productivity for each ecotype showed an over-

all decreasing pattern in yield due to climate change. The spread of decline in yield was the fastest in the early maturing rice, followed by the variety with mid-term growth and long-term grow periods, and the extent of yield decline was the greatest in the early maturing rice variety (Lee *et al.*, 2015a). The results of this study, which were derived from actual cultivation experiments, validated the model prediction results. Thus, it is necessary to continue to study the actual growth response and yield change through global warming simulation experiments for other rice varieties. The growth period, growth state, productivity, and yield changes must be examined along with the physiological properties of the mainly cultivated rice varieties under future global warming conditions. Based on the accumulated data, efforts are urgently required to maintain sustainable productivity through the development of cultivation techniques, including changes in major regional cultivation varieties, development of varieties with a focus on climate change, and changes in sowing and planting seasons.

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