Effects of FACE on Rice Leaf Photosynthesis and Transpiration in a Paddy Field -Changes of Parameters in Farquhar and Ball-Berry Models under Elevated CO₂-

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Abstract

In order to evaluate the effects of FACE (Free air CO₂ enrichment) on the leaf photosynthesis and transpiration of the rice plant, we conducted leaf level measurements by using LI-6400 in both the FACE and the ambient plots through several growing stages. Compared to the ambient plot, the leaf photosynthesis was higher and the leaf transpiration was lower in the FACE plot. The Farquhar model and Ball-Berry model were applied to identify the physiological properties of the rice plants both in the FACE and ambient conditions. The parameters of the models were determined by fitting the models to the observed data. With the decided parameters, we assayed the sensitive analysis for the leaf photosynthesis and transpiration. Applying the identical atmospheric CO₂ into the model, the leaf photosynthesis simulated in the FACE leaf was lower than that of the ambient leaf, while the transpiration simulated in the FACE leaf was higher than that of the ambient leaf.

These results suggest that the potential activity of the photosynthesis decreased and the potential activity of the transpiration increased in the FACE leaves.

Key words: Farquhar and Ball-Berry models, Leaf photosynthesis, Leaf transpiration

1. Introduction

In order to evaluate the effects of the elevated CO₂ on leaf photosynthesis and transpiration, we observed leaf photosynthesis and transpiration both in ambient and elevated CO₂ conditions. The experiment was made at the upper (upper leaf) and lower parts of the plant (lower leaf) under various light intensities. Therefore, the dependences of the leaf position and light intensity were reflected in the results. The observed data were applied to the model so that the plants physiological parameters were obtained. Thus, we discussed the change of the parameters to understand not only the superficial changes but also the physiological changes of the rice plant induced by the elevated CO₂.

2. Materials and Methods

2.1 Rice FACE experiment

The rice FACE (Free Air CO₂ Enrichment)

experimental system was placed in a rice field (*Oryza sativa* L. cv. Akitakomachi) which was located in Shizukuishi, Iwate, Japan (39°38'N, 140°57'E). The CO₂ treatment was established by means of the octagonal FACE ring (Okada *et al.*, 2001) in the elevated CO₂ plot (FACE). The ambient plot (ambient) where the atmospheric CO₂ was not controlled was placed far enough not to be affected by the FACE system. The average atmospheric CO₂ concentrations were 350 ppm in the ambient and 550 ppm in the FACE plots.

2.2 LI-6400 measurement

The leaf photosynthesis and transpiration were measured with a portable photosynthesis system (LI-6400; Li-COR, Lincoln, NE, USA). The measured leaves were selected from the upper and lower leaves. The measurement was made through the daytime (7:00-18:00 JST), repeating the FACE and ambient plots continuously so that we could obtain the data under various PPFD (photosynthetic photon flux density) conditions. These were

measured on July 11-12; the early tillering stage, July 22; the tillering stage, August 1-6; the heading stage, August 13; the flowering stage and September 12-15; the milking stage. Simultaneously, the PPFD to which the leaves were exposed were obtained from the quantum sensor mounted on the LI-6400. The SPAD value which was supposed to reflect the chlorophyll density of the leaf was also measured with the SPAD meter (SPAD-501; Minolta Camera Co., Ltd. JAPAN), concurrently with the LI-6400 measurement.

3. Results

3.1 Change in the leaf photosynthesis and transpiration due to the elevated CO₂

In order to quantify the change in the leaf photosynthesis, the non-rectangular hyperbolic light response function in the form of Eq. (1) was fitted to the observed photosynthesis.

$$A_{\max} = (\alpha A + A_{\max} - \{(aQ + A_{\max})^2 - 4aQ\theta A_{\max}\}^{0.5}) / 2\theta - R, \quad (1)$$

where, A is the photosynthesis, $A_{\max}$ is the asymptotic limit of the photosynthesis (equal to the maximum datum), R is the mitochondrial respiration, α is the initial slope, Q is the incident PPFD and θ is the convexity of the function.

Table 1 Differences of the leaf photosynthesis and transpiration of the upper or lower leaf between the FACE and ambient plant, calculated by the non-rectangular hyperbolic function adapted to the observed photosynthesis and the transpiration data sets at 500 and 2000 $\mu\text{mol m}^{-2}\text{s}^{-1}$ PPFD light intensities respectively.

Stages 1-5 indicate July 11-12, July 22, Aug. 1-6, August 13 and Sep. 12-15 respectively. (↑; increased value with the FACE, ↓; decreased value with the FACE)

Photosynthesis difference ($\mu\text{mol m}^{-2}\text{s}^{-1}$)					
Stage	Upper leaf		Lower leaf		<i>p</i>
	PPFD ($\mu\text{mol m}^{-2}\text{s}^{-1}$)				
	500	2000	500	2000	
1	-2.169	3.917	0.813	5.540	0.234 ↑
2	3.697	4.435	2.940	3.390	0.000 ↑
3	0.794	2.151	0.306	2.905	0.102 ↑
4	0.814	5.963	-5.924	-9.847	0.522 ↓
5	0.674	-0.979	-2.057	-1.963	0.087 ↓
<i>p</i>	0.412 ↑	0.009 ↑	0.603 ↓	1.000 ↑	0.373 ↑
Transpiration difference (mm h^{-1})					
1	-0.003	0.006	0.026	0.058	0.112 ↓
2	-0.003	-0.087	-0.084	-0.096	0.002 ↓
3	-0.075	-0.081	-0.167	-0.078	0.000 ↓
4	-0.065	-0.102	-0.111	-0.253	0.001 ↓
5	-0.037	-0.054	-0.025	0.051	0.484 ↓
<i>p</i>	0.139 ↓	0.001 ↓	0.032 ↓	0.263 ↓	0.000 ↓

By using this function, we calculated the difference of the leaf photosynthesis at both irradiances of 500 and 2000 $\mu\text{mol m}^{-2}\text{s}^{-1}$ PPFD (Table 1). The change in the leaf transpiration was also investigated as well as the leaf photosynthesis. The T-test was applied to these differences to verify them across each light intensity, leaf position and growing stage.

It was apparent that under the high light irradiance, the FACE caused an increase in photosynthesis in the upper leaf except at the 5th stage ($p=0.009$). Although there was no difference in the leaf photosynthesis between the FACE and ambient in the lower leaf, as a whole, the leaf photosynthesis increased in the FACE to some extent ($p=0.373$).

It was also clear that the leaf transpiration decreased due to the elevated CO₂ through the entire observation term ($p=0.000$).

3.2 The Farquhar & Ball-Berry model application to the leaf photosynthesis and transpiration

The Farquhar model for photosynthesis (Farquhar *et al.*, 1980) and the Ball-Berry model for stomatal conductance (Ball *et al.*, 1987) were utilized as biological models, which were composed of the plants physiological parameters. We applied these models to the observed photosynthesis and transpiration adjusting two parameters: the leaf chlorophyll density and the Ball-Berry coefficient. The leaf chlorophyll density was determined for every SPAD value both in the FACE and ambient respectively, while the Ball-Berry coefficient was calculated for both upper and lower leaves in both the FACE and ambient plants at every observed stage.

The model reproduced the leaf photosynthesis and transpiration successfully (Fig. 1). The determined parameters were shown in Fig. 2. The calculated leaf chlorophyll density was lower in the FACE leaves than in the ambient leaves. As the plant grew, the difference of the leaf chlorophyll density between the FACE and ambient became more apparent. Overall, the Ball-Berry coefficient was higher in the FACE leaves than in the ambient leaves.

The leaf chlorophyll density estimated by the model was linearly correlated to the measured SPAD value (Fig. 3). The 10% discrepancy ($p=0.555$) of the leaf chlorophyll density indicates possible effects of other parameters which were regarded as the same values both in the FACE and ambient.

4. Discussions and Conclusions

4.1 Sensitivity analysis of the parameter

We assayed the sensitive analysis of the model parameters: the atmospheric CO₂ concentration, the leaf chlorophyll density and the Ball-Berry

coefficient, for the leaf photosynthesis and transpiration. The percentage increments of either the leaf photosynthesis or transpiration were calculated by changing one or two parameters from that of the ambient to the FACE under both 500 and 2000 $\mu\text{mol m}^{-2}\text{s}^{-1}$ PPFD, while other parameters were unchanged.

Figure 4(a), (b) show the percentage increment of the photosynthesis and transpiration when the photosynthesis and transpiration of the FACE and ambient leaves were calculated under the same CO_2 atmospheric condition (350 ppm). As a whole, it was apparent that the simulated photosynthesis decreased, while the simulated transpiration of the upper leaf increased slightly. However, there was no difference in the simulated transpiration in the lower leaf.

The elevated CO_2 contributed to the increase of the leaf photosynthesis and to the decrease of the transpiration, especially in the 2000 $\mu\text{mol m}^{-2}\text{s}^{-1}$ PPFD (Fig. 4 (c), (d)).

Figure 4 (e), (f) show that the decrease of the leaf chlorophyll density caused the decreases of the leaf photosynthesis and transpiration. These figures also indicate that the extent to which the change in the leaf chlorophyll density affected the leaf photosynthesis and transpiration was dependent on the light intensity.

The increase of the Ball-Berry coefficient caused the increase of the leaf transpiration in the upper leaf (Fig. 4 (g), (h)). However, there was no obvious difference in the lower leaf.

Fig. 3 Relationships between the SPAD and the leaf chlorophyll density calculated for both FACE and ambient leaves. The solid line represents the regression line in the FACE while the dashed line that in the ambient. (●; FACE, □; ambient)

In conclusion, under the elevated CO_2 , the photosynthesis activity decreased, while the transpiration activity increased. However, under the elevated CO_2 , the direct effect of the CO_2 exceeded the effect caused by the decrease of the leaf chlorophyll density, so that the leaf photosynthesis increased. Although the increase of the Ball-Berry coefficient contributed to the increase of the leaf transpiration, the effect of the elevated CO_2 and an ancillary effect inherent in the change of the leaf chlorophyll density caused the decrease of the leaf transpiration under the FACE conditions.

Fig. 1 Model verification by regression analysis
(a) The calculated leaf photosynthesis (A_c) vs. measured leaf photosynthesis (A_{Obs}).
(b) The calculated leaf transpiration (E_c) vs. measured leaf transpiration (E_{Obs})

Fig. 2 The seasonal changes of the parameters: (a) the leaf chlorophyll density (b) the Ball-Berry coefficient, calculated both for the FACE and ambient leaves. The solid line represents the value of the upper leaf, while the dashed line that of the lower leaf. (●; FACE; □; ambient)

Fig. 4 The sensitive analyses of the parameters : (a), (b) the physiological parameters, (c), (d) the atmospheric CO_2 , (e), (f) the leaf chlorophyll density and (g), (h) the Ball-Berry coefficient, in the change of the leaf photosynthesis and transpiration. The dashed line represents the value at PPFD of $2000 \mu\text{mol m}^{-2}\text{s}^{-1}$, while the solid line that at PPFD of $500 \mu\text{mol m}^{-2}\text{s}^{-1}$. (●; upper leaf, □; lower leaf)

4.2 Adverse results in the lower leaf

In the lower leaf, sometimes the effect of the dramatic decrease of the leaf chlorophyll density exceeded that of the elevated CO_2 on the leaf photosynthesis. Therefore, we could not find any difference in the lower leaf photosynthesis between FACE and ambient leaves (Table 1). The decrease of the leaf chlorophyll density was also supposed to cause the decrease of the leaf transpiration to some extent (Fig. 4 (f)). This decrease of the lower leaf transpiration was accounted for by the decrease of the Ball-Berry coefficient from the tillering stage to the heading stage in the FACE leaves (Fig. 2 (b)).

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