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Is photosynthetic acclimation to free-air CO_2 enrichment (FACE) related to a strong competition for the assimilatory power between carbon assimilation and nitrogen assimilation in rice leaf?

Z.-H. YONG[*], G.-Y. CHEN[*], D.-Y. ZHANG[*], Y. CHEN[*], J. CHEN[*], J.-G. ZHU[**], and D.-Q. XU[*,***]

Institute of Plant Physiology and Ecology, Shanghai Institutes for Biological Sciences, Chinese Academy of Sciences, and Graduate School of the Chinese Academy of Sciences, Shanghai 200032, China[*]
State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, Nanjing 210008, China[**]

Abstract

Net photosynthetic rate (P_N) of leaves grown under free-air CO_2 enriched condition (FACE, about 200 µmol mol^{-1} above ambient air) was significantly lower than P_N of leaves grown at ambient CO_2 concentration (AC) when measured at CO_2 concentration of 580 µmol mol^{-1}. This difference was found in rice plants grown at normal nitrogen supply (25 g m^{-2}; NN-plants) but not in plants grown at low nitrogen supply (15 g m^{-2}; LN-plants). Namely, photosynthetic acclimation to FACE was observed in NN-plants but not in LN-plants. Different from the above results measured in a period of continuous sunny days, such photosynthetic acclimation occurred in NN-plants, however, it was also observed in LN-plants when P_N was measured before noon of the first sunny day after rain. Hence strong competition for the assimilatory power between nitrogen (N) and carbon (C) assimilations induced by an excessive N supply may lead to the photosynthetic acclimation to FACE in NN-plants. The hypothesis is supported by the following facts: FACE induced significant decrease in both apparent photosynthetic quantum yield (Φ_c) and ribulose-1,5-bisphosphate (RuBP) content in NN-plants but not in LN-plants.

Additional key words: apparent quantum yield; carboxylation efficiency; net photosynthetic rate; nitrogen supply; *Oryza*; ribulose-1,5-bisphosphate regeneration.

Introduction

Leaf photosynthesis of C_3 plant increases when the leaf is exposed to an elevated CO_2 concentration. The stimulatory effect of high CO_2 concentration on photosynthesis, however, declines gradually with prolonging the high CO_2 exposure time. Moreover, after long-term exposure net photosynthetic rate (P_N) in plants grown at high CO_2 concentration is significantly lower than that in plants grown in ambient air (AC) when measured at the same CO_2 concentration. This phenomenon is called acclimation or down-regulation of photosynthesis.

Photosynthetic acclimation is often observed both in controlled environment (DeLucia *et al.* 1985, Spencer and Bowes 1986, Xu *et al.* 1994a,b) and in the field (Arp 1991, Adam *et al.* 2000, Ainworth *et al.* 2003). However, some experiments show no acclimation to high CO_2 concentration (Radin *et al.* 1987, Herrick and Thomas 2001). For the occurrence of photosynthetic acclimation, nitrogen (N) supply level seems to be one of the important determinants. Some studies showed that the photosynthetic acclimation was more obvious under sub-optimal N supply (Wong 1979, Drake *et al.* 1997) and there was no photosynthetic acclimation when N supply was adequate

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[***] Author for correspondence; fax: +86-21-54924015, e-mail: dqxu@sippe.ac.cn

Abbreviations: AC – ambient CO_2 concentration; C – carbon; CE – carboxylation efficiency; C_i – intercellular CO_2 concentration; FACE – free-air CO_2 enrichment; J_{max} – maximum *in vivo* electron transport rate; N – nitrogen; NR – nitrate reductase; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; RuBP − ribulose-1,5-bisphosphate; V_{cmax} – maximum *in vivo* carboxylation rate; Φ_c – apparent quantum yield of carbon assimilation.

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(Stitt and Krapp 1999). In fact, the photosynthetic acclimation may be an indirect effect of N, and is dependent on the sink-source balance of plants (Rogers *et al.* 1998). Moreover, when N was supplied in direct proportion to plant growth, elevated CO_2 did not induce the acclimation (Farage *et al.* 1998). Seneweera *et al.* (2002) have suggested that under free-air CO_2 enrichment (FACE) conditions the photosynthetic acclimation in rice flag leaves is due to a large demand for N, relative to N supply from root uptake and remobilization from leaves, at the reproductive stage. It seems that inadequate N supply to N demand is an essential prerequisite for occurrence of photosynthetic acclimation. Nevertheless, we found that under adequate N supply the photosynthetic acclimation to high CO_2 also occurred in rice leaves and was related to both ribulose-1,5-bisphosphate (RuBP) carboxylation limitation and RuBP regeneration limitation (Chen *et al.* 2005). The relationship between N supply and photosynthetic acclimation to high CO_2 concentration may be more complicated than what was imagined before.

In order to explore this relationship the photosynthetic responses of rice plants to long-term FACE were examined at two N supply levels: 25 g m^{-2} – normal N supply for local rice production (NN) and 15 g m^{-2} – low N (LN) supply. We found that the photosynthetic acclimation to FACE occurred in rice leaves under NN but not under LN. Based on the changes in the apparent quantum yield and RuBP content we suppose that an excessive N supply-induced strong competition for the assimilatory power between N and carbon (C) assimilation leads to the photosynthetic acclimation in FACE leaves of NN-plants.

Materials and methods

FACE site and rice growth: The Chinese rice FACE facilities were located at Anzhen village (120°27'51"E, 31°37'24''N), Wuxi city in 2001–2003 and were transferred to Xiaoji village (119°42'0"E, 32°35'5''N), Yangzhou city in 2004–2005, in Jiangsu Province, East China. Both sites are in a typical region for rice production in China. The running and controlling systems of the facilities were transferred from Japanese rice FACE site (Okada *et al.* 2001). A full description of Chinese rice FACE facilities has been provided by Liu *et al.* (2002). Briefly, in the experimental field there were 8 rings with a 12 m-diameter. Among them, three rings were sprayed by pure CO_2 as FACE treatment, and the others were in common atmosphere as ambient (AC) control. The intervals between FACE and AC rings were more than 90 m. Target CO_2 concentration in the centre of FACE rings was 200 µmol mol^{-1} above AC. CO_2 enrichment of rice plants in FACE rings was commenced immediately after transplanting, and applied continuously during day and night until harvesting.

Rice (*Oryza sativa* L.) cultivar Japonica 9915 used in this study is a new one planted commonly in this region. Its growth duration (from transplanting to harvesting) is about 130 d (from medium June to medium October). Its cultivation was performed with typical agronomic management techniques for this region. Seeds of Japonica 9915 were germinated in a seedbed without a layer of water in AC, and the seedlings were transplanted into the plots of experimental field on June 13. The planting density was 17×25 cm. N was supplied as urea (NH_2CONH_2) (85 %) and $(NH_4)_2HPO_4$ (15 %) at 15 g N m^{-2} (LN, relative to NN supply of 25 g N m^{-2} in local rice field, may be near optimal for rice growth and development), with 40 % of N supplied as a basal dressing, 20 % on the 5th day after transplanting , and 40 % at the panicle initiation stage. Phosphorus was applied at 7.5 g(P_2O_5) m^{-2}. The soil was flooded before transplanting, and the water layer of 5 cm above soil level was maintained except when the field was drained several times.

Gas exchange measurements were made *in situ* using a portable gas analysis system *LI-6400* (*LI-COR*, USA) with 10–12 fully expanded flag leaves in each ring during 10:00 to 14:30 (Beijing time) in mid-August (heading stage), early September (early filling stage). These measurements were performed between FACE and AC rings in turn. In the measurements, CO_2 concentration was controlled at 580 µmol(CO_2) mol^{-1} with *LI-COR* CO_2 injection system, and a saturating photosynthetic photon flux density (PPFD) of 1 200 µmol m^{-2} s^{-1} from a *LI-COR* LED irradiation source was supplied. Air temperature of leaf chamber was maintained at about 30 ºC. Before recording data, the measured leaves were kept in the leaf chamber for 2 min to reach a steady state of photosynthesis. Then, some of these leaves were used to measure the apparent quantum yield of carbon assimilation (Φ_c) (Xu *et al.* 1987) and carboxylation efficiency (CE) (Farquhar *et al.* 1980, Caemmerer and Farquhar 1981). In Φ_c measurement, CO_2 concentration was kept at 580 µmol mol^{-1}, and the PPFD was set at 160, 135, 110, 85, 60, and 35 µmol m^{-2} s^{-1} in turn. For CE measurement, PPFD was kept at 1 200 µmol m^{-2} s^{-1}, and CO_2 concentration was controlled with *LI-COR* CO_2 injection system set at 250, 200, 150, 100, 50, and 25 µmol mol^{-1} in turn. For making the curve of photon-saturated P_N to intercellular CO_2 concentration (C_i), P_N values were measured at CO_2 concentrations of 250, 200, 150, 100, 50, 380, 480, 580, 650, 750 and 900 µmol mol^{-1} in turn, and PPFD was kept at 1 200 µmol m^{-2} s^{-1} during the measurement. The maximum *in vivo* carboxylation rate (V_{cmax}) and the maximum *in vivo* electron transport rate (J_{max}) were calculated on the basis of P_N/C_i curve data (Farquhar *et al.* 1980, Caemmerer and Farquhar 1981).

Leaf sampling: All leaf samples used in biochemical analysis were collected during 10:30 to 13:00 in the light. The detached leaf samples were excised to 5-cm long segments (excluding the tip and base) and their areas were measured with a portable leaf area meter *LI-3000A*. Then, the leaf segments were immediately dropped in liquid N_2, taken back to laboratory with dry ice, and preserved at –80 °C until biochemical analysis.

RuBP content: The RuBP from rice leaves was extracted using the method of Vu *et al.* (1997), while the RuBP content was calculated on the basis of the amount of glycerate-3-phosphate formed in RuBP carboxylation reaction catalyzed by ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) purified from tobacco leaves. The determination of glycerate-3-phosphate was made according to Voordouw *et al.* (1984).

ATP content: The fresh leaf segments collected in the light were immediately cut into small pieces (about 1 mm^2), and put into a boiling solution of $MgSO_4$ (1 mM) at once. Then, the solution was kept at 100 °C for 10 min. The supernatant of ATP extract after centrifugation was preserved at –40 °C for detection. Measurement of ATP content was performed using a luminometer (*FG 300*) with a kit of luciferase-luciferin (the luciferase was obtained from firefly) made by Shanghai Institute of Plant Physiology and Ecology according to the method described in the manual of the kit (Wang and Gu 1988).

Statistical analysis of all data, including mean, standard error, and *t*-tests, was made with *Sigma Plot 9.0* (*SPSS*, USA).

Results

Effects of FACE on P_N: Under NN, P_N in FACE leaves was significantly lower than that in AC leaves when measured at the same CO_2 concentration [580 µmol(CO_2) mol^{-1}], indicating that photosynthetic acclimation occurred (Fig. 1*A*). Also, under higher N supply (35 g m^{-2}) a similar result was obtained in 2003 (data not shown). However, under LN (15 g m^{-2}) no acclimation was observed in FACE leaves (Fig. 1*B*). Surprisingly, in the morning of the first sunny day after rain the photosynthetic acclimation was observed in LN-plants (Fig. 1*C*).

The two response curves of P_N/C_i for AC and FACE leaves were clearly separated, especially in high C_i region in NN-plants (Chen *et al.* 2005). In LN-plants, however, the two curves were very similar (Fig. 2*A*). In LN-plants there was no significant difference in V_{cmax} and J_{max} between FACE and AC leaves, but the two parameters measured in the morning of the first sunny day after rain in FACE leaves were significantly lower, compared with those in AC leaves (Table 1).

Effects of FACE on carboxylation efficiency (CE), Φ_c, and RuBP and ATP contents: Different from NN-plants, LN-plants grown under FACE had a basically unchanged CE (initial slope of P_N/C_i curve at low CO_2 concentration), compared with that of plants grown in AC (Fig. 3). In NN-plants, Φ_c of FACE leaves was much lower than in AC leaves, but it had no significant change in FACE leaves of LN-plants (Fig. 4). RuBP content was much lower in FACE leaves of NN-plants, while it did not basically change in FACE leaves of LN-plants (Fig. 5). ATP content of FACE leaves decreased in the NN-plants but not in LN-plants compared with those of AC leaves. However, the ATP content in FACE leaves of LN-plants collected in the morning of the first sunny day after rain was significantly lower than that in AC leaves of LN-plants (Fig. 6).

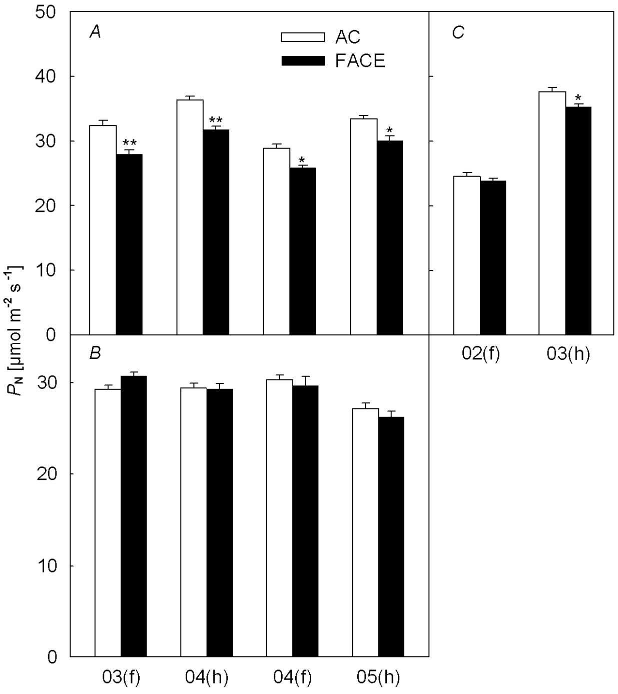

Fig. 1. P_N values of CO_2-enriched, FACE (*black columns*) and ambient, AC (*white columns*) rice flag leaves measured at the same CO_2 concentration (580 µmol mol^{-1}). Means of thirty leaves in three rings with SE expressed as *vertical bar*. The rice plants were grown under normal N, NN (*A*) and low N, LN (*B*, *C*) supply. Measurements of *A* and *B* were made on continuous sunny days, and it was also clear before the measurement day, while measurement of *C* was made before the noon of the first sunny day after rainy days. $^{*}p<0.05$, $^{**}p<0.01$. *The numbers below abscissa* represent the years in which measurements were made, and (h) and (f) means that measurements were made at the heading and filling stages, respectively.

Table 1. Effects of FACE on V_{cmax} and J_{max} in the flag leaves of low N (LN) supplied rice plants. V_{cmax} and J_{max} were calculated on the basis of the P_{Nsat}/C_i curve data in Fig. 2. The P_N values of AC and FACE leaves were measured on a clear day after continuous sunny days, and the P_N values of AC ar and FACE ar were measured before noon of the first day after rain.

	AC	FACE	AC ar	FACE ar
V_{cmax} [μmol(CO$_2$) m^{-2} s^{-1}]	99.0 (3.7)	93.8 (5.3)	94.5 (4.0)	75.1 (3.1)
J_{max} [μmol m^{-2} s^{-1}]	150.0 (6.2)	145.0 (8.4)	147.7 (15.0)	98.6 (14.1)

Discussion

In the previous study we demonstrated that photosynthetic acclimation to FACE occurs in rice leaves developed at NN-supply, and suggested that the acclimation is related to both RuBP carboxylation limitation and RuBP regeneration limitation (Chen *et al.* 2005). Experimental results of the present study show that no photosynthetic acclimation occurs in FACE rice leaves developed at LN-supply (Fig. 1*B*). This may imply that there is neither RuBP carboxylation limitation nor RuBP regeneration limitation in FACE leaves under LN-supply. The following facts support the deduction: (*1*) The P_{Nsat}/C_i curves were almost identical for FACE and AC leaves (Fig. 2*A*). (*2*) No significant change occurred in V_{cmax} and J_{max} of FACE (Table 1). (*3*) CE in FACE leaves did not decline significantly compared with that in AC leaves (Fig. 3).

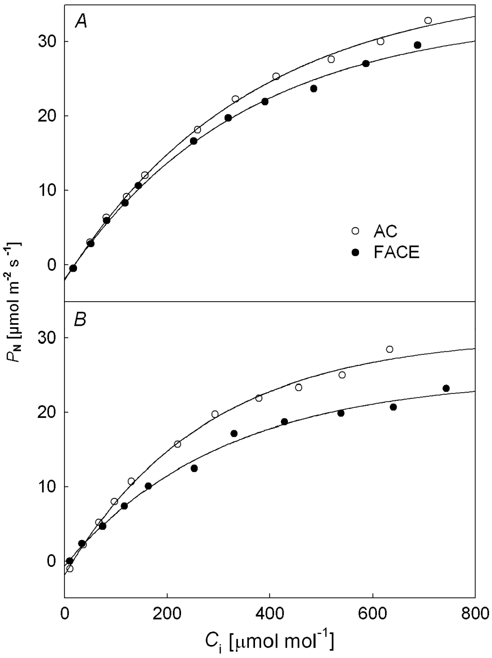

Fig. 2. Responses of photon-saturated net photosynthetic rate (P_N) to intercellular CO$_2$ concentration (C_i) in the flag leaves of low N-supplied (LN) rice plants grown in ambient, AC (*open circles*) and FACE (*filled circles*) rings. Measurements were made at the heading stage and the Xiaoji site in 2005. Measurements of *A* were made on continuous sunny days, while measurements of *B* were made before the noon of the first sunny day after rain.

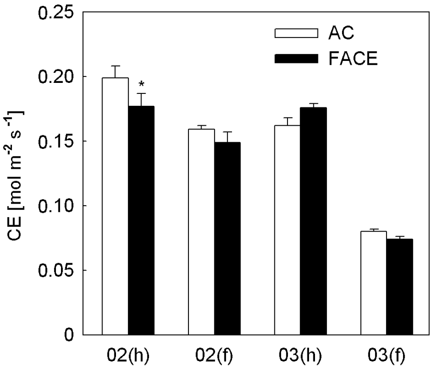

Fig. 3. Effect of FACE on carboxylation efficiency (CE) in the flag leaves of low N-supplied (LN) rice plants. Each value in this figure is the mean of five leaves with SE expressed as *vertical bar*.

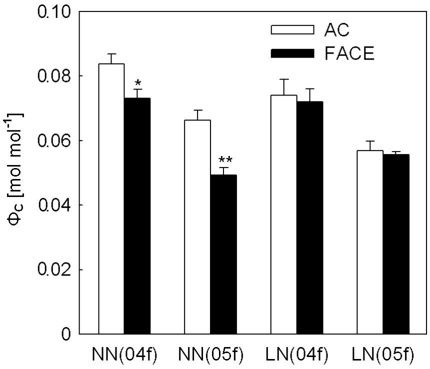

Fig. 4. Effect of FACE on apparent quantum yield of carbon assimilation (Φ_c) in rice flag leaves. Measurements were made at the same CO$_2$ concentration (580 μmol mol^{-1}). Each value in this figure is the mean of five leaves with SE expressed as vertical bar. NN: normal N supply; LN: low N supply.

In the light, both C assimilation and N assimilation (such as nitrate reduction and ammonia assimilation) occur simultaneously in plant leaves. The two kinds of assimilation reactions require the assimilatory power, ATP and NADPH. For example, when 1 CO$_2$ molecule is assimilated into saccharide (*e.g.* triose), at least 3 ATP and 2 NADPH molecules are required. Reducing 1 NO$_3^-$ to NO$_2^-$ consumes 1 NADH or NADPH molecule and reducing 1 NO$_2^-$ to NH$_4^+$ consumes 6 Fd (reduced ferredoxin) molecules, while assimilating 1 NH$_4^+$ into glutamine consumes 1 ATP molecule (Iglesias *et al.* 2005). Therefore, the assimilatory power as well as Fd formed in photosynthetic electron transport and coupled photophosphorylation processes are used not only in C assimilation but also in N assimilation. Thus there is a competition for the assimilatory power between C and N assimilations in the leaf. Naturally, such a competition is stronger under ample C (FACE) and/or N supply conditions used in our experiments.

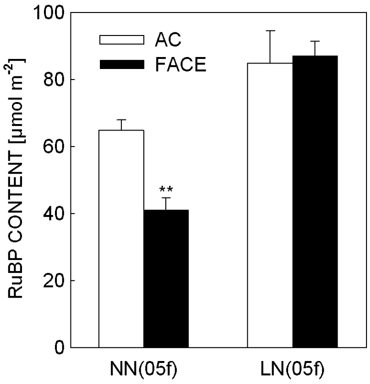

Fig. 5. Effect of FACE on RuBP content in the flag leaves of low (LN) and normal (NN) N-supplied rice plants. Each value in this figure is the mean of six measurements with SE expressed as *vertical bar*. Five leaves were used in each measurement.

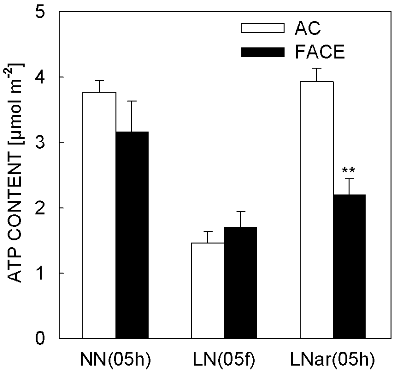

Fig. 6. Effects of FACE on ATP content in the flag leaves of low (LN) and normal (NN) N-supplied rice plants. The leaves of NN and LN were collected on a clear day after continuous sunny days, while those leaves of LNar were collected before noon of the first sunny day after rain. Each value in this figure is the mean of six measurements with SE expressed as *vertical bar*.

From some studies (Hussain *et al.* 1999, Seneweera *et al.* 2002) we deduced that N supply of *ca.* 12 g m^{-2} is sufficient for growth and development of rice plant. Then, the two N levels, 25 and 15 g m^{-2}, used in our experiments, are super-optimal or excessive and near optimal, respectively, for rice growth and development though they are considered as normal and low N supply for local rice production. Therefore, our experimental results that photosynthetic acclimation to FACE was observed in NN-plants (Chen *et al.* 2005) but not in LN-plants (Fig. 1) may be explained by a hypothesis of strong competition for the assimilatory power between C assimilation and N assimilation. Under normal N supply, N nutrient is practically excessive for growth and development of rice plant. And assimilating the excessive N inevitably consumes more assimilatory power than under LN (it is practically near optimal) supply, leading to a decline in P_N due to deficiency of the assimilatory power available for C assimilation. This can explain the photosynthetic acclimation observed in rice plants under NN-supply. Compared with the status under NN-supply, the competition of N assimilation for the assimilatory power is weaker under LN-supply so that it can not induce a significant decline in P_N, *i.e.* photosynthetic acclimation.

The Φ_c, RuBP, and ATP content measurements supported the hypothesis. We observed that under NN-supply the Φ_c in FACE leaves was remarkably decreased compared with that in AC leaves, but it had no significant change in FACE leaves under LN-supply (Fig. 4). This is obviously due to that an increase in the portion of the assimilatory power used in N assimilation under excessive N supply inevitably leads to a decrease in the portion of the assimilatory power used in C assimilation. Then, the Φ_c expressed in amount of fixed carbon declines in FACE leaves under NN-supply. The significant decline in RuBP content of FACE leaves of NN-plants (Fig. 5) could also be explained by the above mentioned strong competition between N and C assimilations for the assimilatory power. Under FACE and excessive N supply the strong competition may induce a strong limitation of RuBP regeneration due to the shortage of assimilatory power, resulting in the decrease of RuBP content in FACE leaves of NN-plants. Nevertheless, under FACE and low or optimal N supply the competition of N and C assimilations for the assimilatory power is weak. So the decline in RuBP content of FACE leaves does not occur in LN-plants (Fig. 5). The fact that ATP content of FACE leaves decreased significantly in NN-plants but not in LN-plants (Fig. 6) is also consistent with the above explanation.

Some studies show that the nitrate reductase (NR) protein content and activity increase by two- to three-fold in the light period (Galangau *et al.* 1988), and when leaves are dark-treated, NR is inactivated *via* a two-step process (Bachmann *et al.* 1996). Moreover, a preliminary observation showed that there was almost no NR activity in leaves of some plants when measured in the morning of the first sunny day after rain (data not shown). Therefore, it is supposed that due to active synthesis and activation of NR the strong competition of C and N assimilations for the assimilatory power may occur in FACE-treated LN-plants within the first several hours of the light period of the first sunny day after rainy day(s). Perhaps this is why the photosynthetic acclimation can be observed in FACE leaves of LN-plants after rainy days (Fig. 1*C*). Of course, more experiments are required in order to demonstrate the supposition.

Wheat, unlike rice, displays significant photosynthetic acclimation to FACE under both NN and LN supply (Liao *et al.* 2003). A strong competition for the assimilatory power between N assimilation and C assimilation may exist in wheat under both N supplies and FACE. Perhaps the optimal N level for growth and development of wheat is lower than that of rice so that the LN-supply (15 g m^{-2}) is also excessive for wheat in fact. Some differences between rice and wheat have been reported. For example, wheat leaf had a higher CO_2-saturated P_N and greater cytochrome *f* content, chloroplast fructose-1,6-bisphosphatase activity and RuBP regeneration capacity, as well as greater N-use efficiency for photosynthesis than rice leaf (Sudo *et al.* 2003). The physiological and biochemical bases of the difference in photosynthetic acclimation between rice and wheat should be investigated further.

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