REGULAR PAPER

Evaluation of genotypic variation in leaf photosynthetic rate and its associated factors by using rice diversity research set of germplasm

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Abstract In order to evaluate genotypic variation, we measured leaf photosynthetic rate (Pn) and its associated factors for the rice diversity research set of germplasm (RDRS) selected from the Genebank in National Institute of Agrobiological Sciences (NIAS). Pn showed large genotypic variation from 11.9 to 32.1 $\mu mol\ m^{-2}\ s^{-1}$. The variation in stomatal conductance to CO_2 (G_s) explained about 50% of that in Pn, while that in nitrogen concentration (N) in leaves explained about 35%. The genotype group which mainly consists of aus type indica tended to have higher G_s, and the genotype group which corresponds to japonica had a higher nitrogen concentration (N) in leaves. The relationships of Pn with G_s and N were not significantly different among genotype groups, suggesting photosynthetic efficiencies are similar among genotype groups.

Keywords Carbon isotope discrimination · C_i/C_a: gas conductance · Genotype groups · Indica · Japonica · *Oryza sativa* L. · Nitrogen concentration

Abbreviations

1WAH	1 week after heading
2WBH	2 weeks before heading
Δ	Carbon isotope discrimination
C_i	Intercellular CO_2 concentration
C_a	Ambient CO_2 concentration
DTH	Days to heading from sowing
G_s	Stomatal conductance to CO_2
I1	A genotype group corresponding to aus type indica
I2	A genotype group corresponding to indica except aus
J	A genotype group corresponding to japonica
N	Nitrogen weight per unit leaf area
N%	Nitrogen percentage in leaf dry matter
PAR	Photosynthetically active radiation
Pn	Leaf photosynthetic rate
QTL	Quantitative trait loci
RFLP	Restriction fragment length polymorphism
SSR	Single-sequence repeat
RDRS	Rice diversity research set of germplasm
RubisCO	Ribulose-1,5-bisphosphate carboxylase/oxygenase
VPD	Vapor pressure deficit

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Introduction

Since leaf photosynthetic rate (Pn) is one of the most important traits for rice production, many studies have evaluated its genotypic variation and analyzed its determination factors. For example, Kawamitsu and Agata (1987) measured Pn in 50 rice varieties, and reported a close relationship between Pn and stomatal conductance (G_s). The effect of nitrogen concentration (N) on Pn has also been reported by many investigators (Cook and Evans 1983; Sinclair and Horie 1989). Although breeding efforts decreased depletion of photosynthetic rate during the grain-filling period by increasing N in leaf, potential rate of

photosynthesis have not been improved (Kuroda and Kumura 1990; Sasaki and Ishii 1992). In order to increase the potential Pn, Pn and its associated factors must be analyzed more precisely from the viewpoint of genotype and genetics.

Most rice cultivars are *Oryza sativa* L. and commonly divided into three sub-species, japonica, indica, and javanica. Maruyama and Tajima (1990) measured G_s in 50 cultivars and reported that indica has larger G_s than japonica. Other information about the difference in photosynthetic traits among sub-species is limited. Moreover, other classifications of *Oryza sativa* have been proposed based on the results of genotype analysis using DNA markers. Kojima et al. (2005) conducted a genome-wide restriction fragment length polymorphism (RFLP) survey for 332 accessions of cultivated rice, and classified them into three genotype groups: corresponding to japonica, aus, and indica except aus. Aus is one of the ecotypes of indica, which is generally characterized by early maturity, short statue, drought tolerant, and grown in summer season. Garris et al. (2005) used 169 single-sequence-repeat (SSR) markers and classified 234 accessions of rice into five genotype groups: aromatic, temperate japonica, tropical japonica, indica and aus. The difference in photosynthetic traits among these genotype groups is vague.

Analysis of quantitative trait loci (QTL) provided another measure for analyzing the relationship between genotype and photosynthetic traits. Teng et al. (2004) reported two putative QTLs for Pn using double haploid population derived from a cross between indica and japonica. Some putative QTLs for carbon isotope discrimination (Δ), which is closely linked with process of Pn (Farquhar et al. 1982; Evans et al. 1986), were also reported (Ishimaru et al. 2001; Takai et al. 2006). These procedures may genetically reveal the determination factors of photosynthetic rate. However, it was indicated that effects of QTLs varied with the phenotype and genotype of parents (Mackill 1999; Ashikari and Matsuoka 2006). In order to increase the efficiency of QTL analysis, selection of genotypes for hybridization is important, and information about genotype and phenotype for diverse varieties may help the selection.

The rice diverse research set of germplasm (RDRS) was selected from about 30,000 accessions at the Genebank in National Institute of Agrobiological Sciences, Japan (NIAS), being expected as sufficiently diverse, yet sufficiently small research set, to enable the analysis of basic differences among rice varieties (Kojima et al. 2005). The non-biased population from the viewpoint of RFLP markers is also one of the features of RDRS. This study aimed to evaluate genotypic variation in Pn and its associated factors in RDRS. The difference among genotype groups was also evaluated.

Materials and method

Field experiments and measurements

The experiment was conducted at the experimental field of Kyoto University in 2004. In total, 64 genotypes of RDRS[1] and Takanari, which was one of the highest-yielding varieties in the field (Horie et al. 2003), were planted (Appendix 1). RDRS is divided into three genotype groups: corresponding to japonica (J), aus type indica (I1), and indica except aus (I2). Takanari is classified into I2 group (Ebana, personal communication). All genotypes are seeded on 4 May and transplanted on 26 May. A set of 3×6 plants of each genotype were transplanted at 0.3×0.3 m-spacing. Chemical fertilizer was applied at a rate of 2–14–14 g m^{-2} (N–P$_2$O$_5$–K$_2$O) as a basal, and 1 g m^{-2} N was top-dressed every 20 days.

Single leaf photosynthetic rate (Pn) and stomatal conductance to CO_2 (G_s) were measured with a portable type apparatus for photosynthesis and transpiration measurements (LI-6400, LICOR). The measurement was conducted 2 weeks before heading (2WBH) and 1 week after heading (1WAH) for all genotypes, except ten genotypes which did not reach heading stage (Appendix 1). Pn and G_s of those ten genotypes were measured in early October and used as the data at 2WBH in this study. More than three fully-expanded-uppermost leaves from different plants were measured from 10:00 to 13:00 under light saturated (PAR: 1,500 μmol m^{-2}) and high-relative humidity (60–80%RH) condition.

Immediately after the measurement of Pn, eight fully-expanded-uppermost leaves, including the leaves measured for Pn, were sampled and the leaf area was determined. After the samples were oven-dried at 80°C for 3 days, carbon isotope compositions against a Pee Dee Belemnite (PDB) standard (δ_p, $^{13}C/^{12}C$) and nitrogen concentration (N) of the samples were measured with a mass spectrometer (Delta-S, Thermoquest, USA) equipped with an elementary analyzer (EA1108, FISON, Italy). N was expressed in the weight per unit leaf area (g m^{-2}). Carbon isotope discrimination (Δ) was calculated by the following equation, assuming that carbon isotope composition of the air against a PDB standard (δ_a) was –8‰.

$$\Delta = (\delta_a - \delta_p)/(1 + \delta_a/1000) \tag{1}$$

These measured values were statistically analyzed by one-way analysis of variance with Duncan's test at 5% significant level.

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[1] When RDRS was distributed to us, RDRS consisted of 64 genotypes. The latest RDRS included five genotypes more (Kojima et al. 2005).

Daily weather data during the experiment was obtained from Kyoto Local Meteorological Observatory (Japan Meteorological Agency, 2005) (Fig. 1). Solar radiation was calculated from sunshine hours (Angström 1924) and maximum vapor pressure deficit was calculated from maximum temperature and minimum relative humidity.

Results

Variation of Pn and its associated factors in RDRS

Pn, G_s, C_i/C_a Δ, and N show large variation among genotypes and all traits were normally distributed, suggesting that they are quantitative traits and that the genes controlling the traits were fairly selected by the RFLP survey for RDRS (Fig. 2, also see Appendix 1). The highest value of Pn, 32.1 µmol m^{-2} s^{-1}, was obtained in Tupa729 (No. 53, J, Landrace, Bangladesh) at 1WAH, and the lowest, 11.9 µmol m^{-2} s^{-1}, in Neang Phtong (No. 56, I2, Landrace, Cambodia) at 2WBH. Tupa729 also had the highest value of G_s (Table 1).

G_s in the I1 group was significantly higher than that in the other groups at 2WBH (Table 2). The higher G_s in the I1 group at 2WBH associated with a higher C_i/C_a, and higher Δ. However, as N in the I1 group at 2WBH was significantly lower than in the other groups, Pn was not significantly different among the groups.

At 1WAH, G_s was not significantly different among genotype groups, while N in I1 was lower than that in the others. The lower N in I1 associated with lower Pn though not significantly.

Modern varieties in RDRS gave a higher Pn than landrace varieties. The higher values were associated with higher N of the varieties. The other traits, G_s, Δ and C_i/C_a, did not show any significant difference between modern and landrace varieties. A high-yielding cultivar, Takanari, was included in the top-5 genotypes for Pn, G_s, and N (Table 1).

Relationship among Pn and its associated factors

Table 3 shows the correlation coefficients among Pn and its associated factors. Pn was most closely related with G_s and followed by N. G_s explained about 50% of variation in Pn. The correlation between G_s and N was not significant. C_i/C_a had a relatively close positive correlation with G_s and a low-negative correlation with N. These relations did not vary much with the measured time (2WBH and 1WAH) or by the genotype group (Fig. 3).

Pn was negatively correlated with days to heading (DTH). The negative correlation was mostly derived from that between G_s and DTH (Fig. 4). N was not correlated with DTH.

As previous studies indicated, a significant correlation was observed between Δ and C_i/C_a (Table 3 and Fig. 5). Δ also showed a relatively close correlation with G_s.

Discussion

Leaf photosynthetic rate (Pn) in this study showed large genotypic variation from 11.4 to 32.1 µmol m^{-2} s^{-1}. Since previous studies reported similar variations, e.g., 14.0–32.2 µmol m^{-2} s^{-1} in 50 varieties (Kawamitsu and Agata 1987) and 10–30 µmol m^{-2} s^{-1} in ten varieties (Ohsumi et al. 2007a), the rice diversity research set of germplasm (RDRS) selected by NIAS (Kojima et al. 2005) is thought to almost cover the variation of Pn in rice cultivars. One of the high-yielding cultivars, Takanari, had a higher Pn than standard cultivars (Xu et al. 1997; Ohsumi et al. 2007a), but some landrace genotypes in RDRS had a higher Pn than Takanari. This suggests that Pn can be improved by using genotypic resources in rice cultivars. RDRS may provide useful gene source for the improvement.

Differences among genotype groups were observed in Pn and its associated factors (Table 2). Maruyama and Tajima (1990) reported that indica had a higher G_s than japonica, although such a relation was observed only between I1 and J groups at 2WBH in the present study. Higher carbon isotope discrimination (Δ) in I1 and I2 in this study was also similarly observed in Kondo et al. (2004). The higher Δ may be derived from higher G_s and lower nitrogen concentration (N): higher G_s increases supply of CO_2 and lower N decreases demand of CO_2, both may increase the rate of intercellular to ambient CO_2 concentration (C_i/C_a) and then Δ. These differences among genotype groups imply that genotypes can be genetically classified into phenotype groups, such as extremely higher

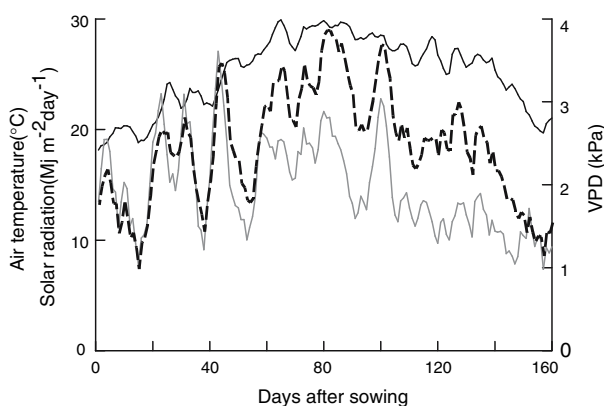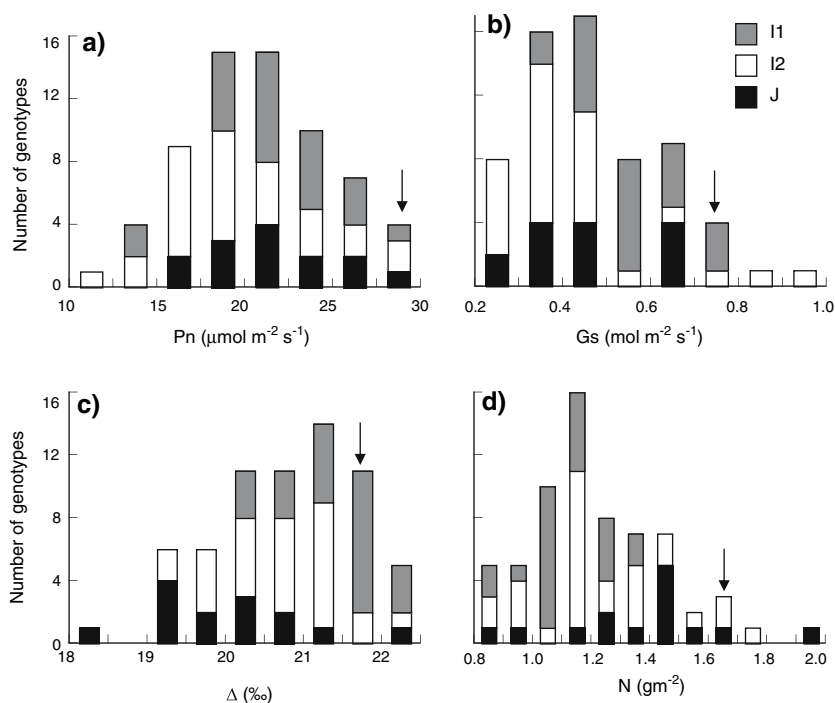**Fig. 1** Daily average air temperature (—), solar radiation (—), and maximum vapor pressure deficit (VPD, - -) during the experiment (5-day moving average)

G_s group, higher N group and higher Pn group. However, the quantitative relations between the factors were not significantly different, e.g. between Pn and stomatal conductance to CO_2 (G_s) (Fig. 3), and between Δ and C_i/C_a (Fig. 5). No significant difference in the quantitative relations indicates that photosynthetic efficiencies, such as kinetic constant of ribulose 1,5-bisphosphate (RuBP) carboxylase (Makino et al. 1987), are similar among genotype groups.

The genotypes which had longer days to heading from sowing (DTH) tended to have lower G_s and then lower Pn than those had shorter DTH (Table 3). Although weather conditions may associate such a tendency, the association was not clear in this study. That is, most genotypes had 80–110 DTH and the weather conditions during the duration were relatively stable in terms of air temperature, solar radiation and vapor pressure deficit (Fig. 1). Ohsumi et al. (2007b) used the same materials and reported that the longer-DTH genotypes tended to have shorter stomatal length. The fact may be associated with the tendency in G_s and Pn.

Stomatal conductance to CO_2 (G_s) explained about 50% of variation of Pn in this study, while N in leaves did less than 35%. Similar results were reported by Kawamitsu and Agara (1987) and Saitoh et al. (1991). G_s is the index of CO_2 supply, and N is the index of the efficiency of photosynthesis. These two factors heighten Pn in different ways. No significant relationship between G_s and N in this study indicates that G_s and N were independently controlled by genes, and able to be improved.

High N in leaves has been one of the important breeding targets since green revolution in 1960s (Rasmusson 1991; Peng et al. 1999). Since higher-N leaves can be distinguished by their dark-green color, recently released cultivars already have higher-N leaves (Cui et al. 2000). In the present study, modern varieties had a higher N than the landrace (Table 2). The improvement of Pn by N is remarkable especially during grain-filling period when leaves of old cultivars start aging process and turns to yellow (Kuroda and Kumura 1990). However, the relation between Pn and N was sparser than that between Pn and G_s as mentioned above. Although significant difference among genotype groups was not observed by regression analysis in the relation between Pn and N, photosynthetic nitrogen use efficiency (PNUE = Pn/N; $\mu mol\ g^{-1}\ s^{-1}$) of I1 at 2WBH was significantly higher than those of the others. The result suggests that PNUE can be improved by breeding and one of the major causes of the higher PNUE is the higher G_s. Horie et al. (2003) explained genotypic difference in Pn by the product of G_s and N percentage in leaf dry matter (N%; g 100 g^{-1}). The correlation between Pn and G_s N% in this study was 0.84 at 2WBH and 0.81 at 1WAH, both of which were slightly higher than those between Pn and G_s and significantly higher than those between Pn and N.

Although the above section indicated that breeding improvement in G_s is necessary to improve Pn, the improvement did not obviously progress in the present because the evaluation of G_s required time and labor. Horie et al. (2003) proposed the product of Δ and N% as an index

Table 1 List of the top-5 genotypes for single-leaf photosynthetic rate (Pn), stomatal conductance to CO_2 (G_s), and nitrogen concentration (N), and the top-3 and the bottom-3 genotypes for ratio of intercellular to ambient CO_2 concentration (C_i/C_a), carbon isotope discrimination (Δ). Values were average of measurements at 2 weeks before heading (2WBH) and at 1 week after heading (1WAH)

Order	No.[a]	Name	Origin	L/M[b]	G[c]	Value
Pn (μmol m^{-2} s^{-1})						
1	53	Tupa 729	Bangladesh	L	J	30.54
2	15	Keiboba	China	L	I2	27.23
3	0	Takanari[d]	Japan	M	I2	27.00
4	8	Ryou Suisan Koumai	China	L	I2	25.86
5	48	Rexmont	USA	M	J	25.53
G_s (mol m^{-2} s^{-1})						
1	53	Tupa 729	Bangladesh	L	J	0.81
2	15	Keiboba	China	L	I2	0.79
3	29	Shoni	Bangladesh	L	I1	0.75
4	19	Shwe Hang Gyi	Myanmar	L	I2	0.72
5	0	Takanari[d]	Japan	M	I2	0.69
N (g m^{-2})						
1	48	Rexmont	USA	M	J	2.03
2	49	Urasan 1	Japan	L	J	1.84
3	61	Padi Kuning	Indonesia	L	I2	1.77
4	0	Takanari[4)]	Japan	M	I2	1.75
5	41	Dianyu 1	China	M	J	1.66
C_i/C_a (mol mol^{-1})						
1	37	Badari Dhan	Nepal	L	I1	0.84
2	38	Nepal 555	India	L	I1	0.83
3	18	Tadukan	Philippines	L	I2	0.83
:						
63	59	Kemasin[e]	Malaysia	L	I2	0.72
64	64	Phulba[e]	India	L	J	0.72
65	51	Tima	Bhutan	L	J	0.69
Δ (‰)						
1	8	Ryou Suisan Koumai	China	L	I2	22.21
2	29	Shoni	Bangladesh	L	I1	22.06
3	38	Nepal 555	India	L	I1	21.87
:						
63	1	Nipponbare	Japan	M	J	19.28
64	51	Tima	Bhutan	L	J	19.27
65	65	Khao Nam Jen[e]	Laos	L	J	18.49

[a] Numbers for RDRS are the same as shown in Kojima et al. (2005)

[b] Landrace or modern varieties

[c] Genotype groups. J: corresponded to japonica; I1: mainly consisted of aus varieties in indica; I2: the other indica

[d] Takanari is not included in RDRS. We numbered here Takanari 0 and classified into I2 group

[e] The cultivars did not reach heading stage. The value is measured in early October

of Pn. Δ may reflect G_s through C_i/C_a. However, Δ N% in this study only explained 57%, 44% and 39% of variation of Pn at 2WBH, 1WAH and in total, respectively (Fig. 6). These insufficient determination factors associate with not strong correlation between Δ and C_i/C_a (Fig. 5). Evans et al. (1986) reported that carbon isotope discrimination deviates from the equation predicted by Farquhar et al. (1982): $\Delta_i = a + (b - a) C_i/C_a$, where Δ_i is the expected discrimination, a is the fractionation occurring due to diffusion in air (4.4‰) and b is the net fractionation caused by RuBP carboxylase and phosphoenolpyrvate carboxylase (29‰). The deviation is proportional to Pn and inversely proportional to internal conductance (Evans et al. 1994). Although the deviation in Evans et al. (1994) was observed

Table 2 Average values of Pn and its associated factors in each genotype group and in modern and landrace varieties[a,b,c]

		Genotype group			Modern	Landrace
		I1	I2	J		
DTH		97 n.s.	103	101	98 n.s.	100
Pn	2WBH	21.7 n.s.	19.8	21.7	24.2 a	20.4 b
	1WAH	19.1 n.s.	21.5	21.3	23.1 a	20.0 b
Gs	2WBH	0.55 a	0.42 b	0.44 b	0.56 n.s.	0.46
	1WAH	0.48 n.s.	0.54	0.45	0.57 n.s.	0.48
C_i/C_a	2WBH	0.81 a	0.78 b	0.76 c	0.78 n.s.	0.78
	1WAH	0.79 n.s.	0.79	0.77	0.79 n.s.	0.79
Δ	2WBH	21.4 a	20.7 b	20.1 c	20.7 n.s.	20.8
	1WAH	20.9 a	20.9 a	20.0 b	20.8 n.s.	20.4
N	2WBH	1.11 a	1.23 a	1.38 b	1.50 a	1.20 b
	1WAH	1.20 a	1.40 b	1.50 b	1.70 a	1.30 b

[a] Abbreviations are the same as in Table 1

[b] Numerals followed by a common letter are not significantly different at 5% level

[c] n.s.: Not significant

Table 3 Correlation coefficients between Pn and its associated factors at 2WBH (a) and 1WAH (b)[a,b]

	DTH	Pn	Gs	C_i/C_a	Δ	N
(a) 2WBH						
DTH	1.00					
Pn	–0.48**	1.00				
G_s	–0.45**	0.76**	1.00			
C_i/C_a	–0.15	0.18	0.69**	1.00		
Δ	–0.56**	0.40**	0.57**	0.65**	1.00	
N	–0.11	0.60**	0.22	–0.28*	–0.02	1.00
(b) 1WAH						
DTH	1.00					
Pn	–0.49**	1.00				
G_s	–0.50**	0.70**	1.00			
C_i/C_a	–0.35*	0.06	0.65**	1.00		
Δ	–0.46**	0.30*	0.55**	0.58**	1.00	
N	–0.05	0.56**	0.13	–0.36**	–0.31*	1.00

[a] Abbreviations are the same as in Table 1

[b] * and ** denotes significance at 5% and 1% level, respectively

Fig. 3 Relationship of leaf photosynthetic rate (Pn) with stomatal conductance to CO_2 (Gs, **a**) and nitrogen concentration (N, **b**). Genotype groups are ●○: I1; ▲△: I2; ✖×: J. The measurement was conducted at 2WBH (solid symbols) and 1WAH (open symbols)
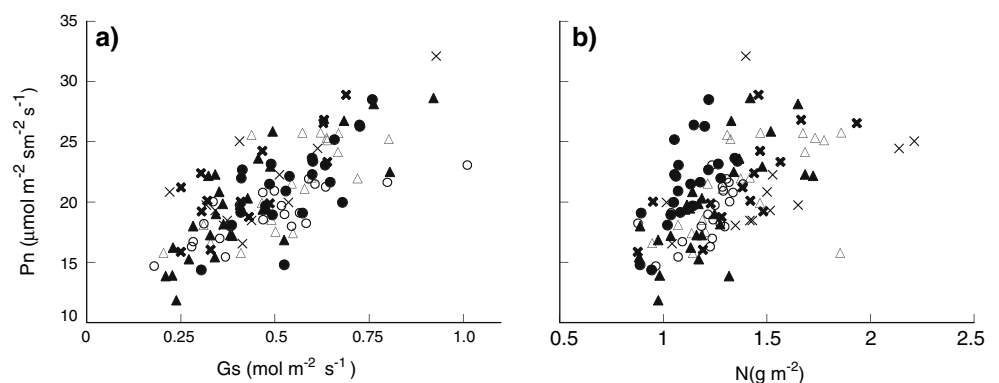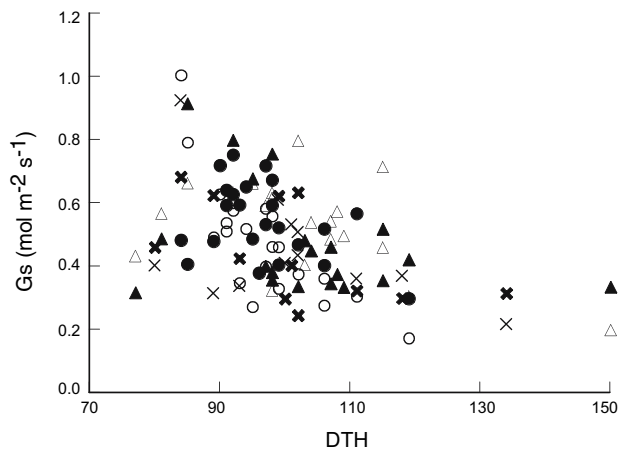
Fig. 4 Stomatal conductance to CO_2 (G_s) as a function of days to heading (DTH). Symbols are the same as in Fig. 3
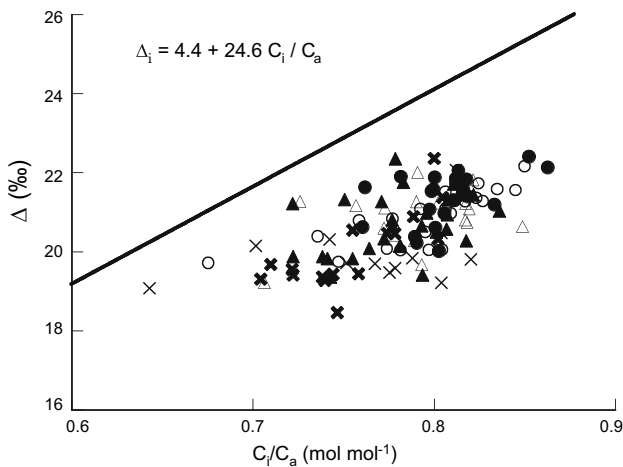

Fig. 5 Relationship between carbon isotope discrimination (Δ) and ratio of intercellular to ambient CO_2 concentration (C_i/C_a). Symbols are the same as in Fig. 3. The line represents the relation predicted by Farquhar et al. (1982)
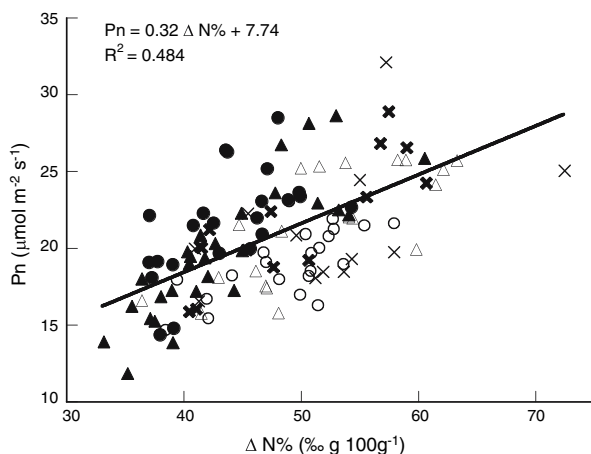

Fig. 6 Leaf photosynthetic rate (Pn) as a function of Δ N%. Symbols are the same as in Fig. 3

by concurrent measurement of carbon isotope discrimination and CO_2 exchange, Hikosaka et al. (1998) reported that Δ measured with leaf dry matter also deviated from Δ_i and that $\Delta_i - \Delta$ was larger in a higher-photosynthetic-capacity species than that in a lower species. Correlation between $\Delta_i - \Delta$ and Pn was also significant at 2WBH in this study but poor ($r = 0.30^*$). Since carbon isotope discrimination occurs not only in photosynthesis but also in respiration, translocation, synthesis of structural materials, and so on, application of the result in Evans et al. (1986) to Δ measured with leaf dry matter may require further study.

This study showed the genotypic variation in Pn and its associated factors. For improvement of Pn, G_s is the key factor. Although it must be considered that G_s is negatively correlated with days to heading, some genotypes in RDRS, such as Keiboba (No. 15, I2, Landrace, China) and Tupa 729 (No. 53, J, Landrace, Bangladesh), may be promising materials for genetic analysis and for breeding.

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