



Photosynthetic efficiency and nitrogen distribution under different nitrogen management and relationship with physiological N-use efficiency in three rice genotypes

Ligeng Jiang¹, Dengfeng Dong, Xiuqin Gan & Shanqing Wei

Key Laboratory of Crop Cultivation and Farming System of Guangxi Province, Guangxi University, Nanning-530005, P.R. China. ¹Corresponding author*

Received 1 June 2004. Accepted in revised form 9 September 2004

Key words: nitrogen distribution in plants, photosynthetic N-use efficiency (Pn/N), Physiological N-use efficiency (PE), rice (*Oryza sativa* L.)

Abstract

Nitrogen fertilization strategies were widely adopted to enhance grain production and improve nitrogen utilization in rice all over the world. For fertilization timing strategy, ear fertilization was usually employed in recent years. For fertilization amount strategy, nitrogen fertilization would continually increase to meet the demands of increasing people for food. However, under heavy ear fertilization as well as great nitrogen amount (NA), physiological N-use efficiency (PE, defined as grain production per unit nitrogen uptake by plants) decreased. Under three NA and two ratios of fertilization given during ear development period to total NA (ear fertilization distribution ratio, EFDR), net photosynthetic rate (Pn), Pn to nitrogen content per unit area (photosynthetic N-use efficiency, Pn/N), nitrogen accumulation in plant tissues and PE of three rice (*Oryza sativa* L.) genotypes, Jinyou 253, Liangyoupeijiu and Baguixiang were screened in the first and second seasons in 2002 so as to understand the fluctuation patterns of Pn/N and nitrogen distribution in leaf blades under great NA & EFDR and relationship with PE in rice. Results showed that under greater NA & EFDR, Pn in flag leaves at heading and plant nitrogen accumulation at maturity always increased and PE & Pn/N always decreased in spite of increased grain production. Rice distributed more nitrogen in leaf blade under greater NA and EFDR. PE indicated significantly ($P < 0.05$) positive relationship with Pn/N and negative relationship with nitrogen distribution ratio in leaf blades at heading and maturity, and no association with Pn in two growing seasons. Results suggested that low PE in rice under great NA and heavy ear fertilization is associated to more nitrogen distribution in leaf blades and decreases in photosynthetic efficiency.

Abbreviations: EFDR – ear fertilization distribution ratio; NA – nitrogen amount; PE – physiological N-use efficiency; Pn – net photosynthetic rate; Pn/N – photosynthetic N-use efficiency.

Introduction

Extravagant nitrogen fertilization in rice has resulted in decrease of physiological N-use efficiency (PE), defined as grain production per unit nitrogen uptake by plants, and serious environ-

mental pollution, scientists have paid more and more attention to PE improvement. There are two main approaches, i.e. improvement in germplasm and resource management, to improve PE in rice. Because of the tremendous variance among genotypes (Broadbent et al., 1987; De Datta and Broadbent, 1990; Jiang et al., 2003), germplasm improvement is commonly regarded

* E-mail: jlg323@263.net

as the most ideal and cheap measure to improve PE in rice. De Datta et al. (1993) and Ladha et al. (1998) have documented the basic relationship of PE in rice genotypes with agronomic and physiological properties such as tiller growth, panicle size, dry matter accumulation, the ratio of leaf weight to plant dry weight, chlorophyll and nitrogen in leaves, grain nitrogen concentration, and leaf nitrogen loss between panicle initiation and harvest. PE in rice genotypes also indicated great association with photosynthetic features, rice genotypes with higher PE acquired higher photosynthetic N-use efficiency (Pn/N, Wu and Tao, 1995) or higher net photosynthetic rate (Pn) at lower Rubisco content (Debabrata et al., 2003).

Nitrogen fertilization strategies were widely adopted to enhance grain production and improve PE in rice all over the world. Timing and amount were the two main aspects of nitrogen fertilization strategies. For timing strategy, nitrogen fertilizer was implemented into paddy field as basal fertilization, or tillering fertilization, or ear fertilization. Heavy ear fertilization during panicle development has been popular to improve population dynamics and enhance panicle weight in China in recent years (Lin, 2000). At IRRI and PRRI, ear fertilization was also adopted to increase grain yield and nitrogen recovery efficiency (Peng and Cassman, 1998). For amount strategy, to achieve 50–70% of fertilizer-N recovery of total quantity applied, N-fertilizer should be applied in the proper amount (Schnier et al., 1990; Peng et al., 1996a, b; Peng and Cassman, 1998). To meet the demands of Asia people for food in 2025, nitrogen fertilization would increase from 7.0 Mt to 19.6 Mt – nearly a 300% increase (Fisher, 1998). However, great nitrogen amount (NA) and heavy ear fertilization usually resulted in low PE in rice (Jiang et al., 2004). Though the relationship of PE in rice genotypes with agronomic and physiological properties has been documented in many literatures, we still have not enough knowledge to understand the mechanism of low PE in rice genotypes under greater NA and heavy ear fertilization. We conducted field experiments with three genotypes, three NA and two ratios of fertilization given during ear development period to total NA (ear fertilization distribution ratio, EFDR) to elucidate the reasons why greater NA

& EFDR resulting in low PE in rice, and our work focused on the fluctuation patterns of flag leaf photosynthetic efficiency and nitrogen distribution in leaf blades under different nitrogen managements and relationships with PE.

Materials and methods

Field experiments

Three rice (*Oryza sativa* L.) genotypes (Baguixiang, Liangyoupeijiu, and Jinyou 253) with obvious difference in PE, selected from thirty rice genotypes in previous experiments (Jiang et al., 2003), were planted in field at Guangxi University Experiment Station, Nanning, China in the first and second seasons in 2002, respectively. The soil was a Laterite contained a total N of 1.9 mg g⁻¹, organic matter of 19.3 mg g⁻¹, exchanged K of 0.104 mg g⁻¹, available Olsen P of 0.052 mg g⁻¹, efficient Si of 0.046 mg g⁻¹, extractable NH₄⁺-N of 0.156 mg g⁻¹ and pH of 6.24. To acquire PE of these three genotypes under different NA and EFDR, three NA were implemented as 0 g N m⁻², 9.8 g N m⁻² and 15.7 g N m⁻² for each genotype, and for each of the NA, two EFDR i.e. 1/3 and 2/3, were implemented. The ear fertilization was split into two applications, the first at ear emergence stage and the second at the day seven after the first ear fertilization. The remaining N was incorporated into the fields as basal before transplanting. Besides the basal N, 11.8 g m⁻² K and 3.0 g m⁻² P were applied as basal fertilization. This experiment was a split-split design, with genotype as main plot, NA as the subplot and EFDR as the sub-subplot and with three replications. Two 4-leaf-age old seedlings per hill were transplanted at the hill space of 13 cm × 30 cm. Low banks around the sub-subplot of 14 m² size were made to prevent penetration of fertilizer nutrients across the plots. Other management practices followed the local production standard.

Sampling and measurement

At heading stage, 20 flag leaves were collected from each plot for nitrogen content measurement. After area measurement with a Laser Area Meter (CI203, USA), leaves were

oven-dried at 80 °C till constant weight, and nitrogen content were determined with a VAP50 Kjeldahlmeter (Gerhart, Germany). At the same time, net photosynthetic rate (Pn) of about seven flag leaves were measured in field with a portable photosynthetic system (CID310, USA) at PPFD of 1000 $\mu\text{mol m}^{-1} \text{s}^{-1}$, leaf temperature of 30 °C, mass flow of 0.3 $\text{mol m}^{-2} \text{s}^{-1}$. At heading and maturity, 30 hills of plants were investigated for calculation of the average panicle numbers per hill. Then, four representative hills of plants from each plot based on the investigation were separately sampled and divided into leaf blades, stems plus sheathes, and panicles. The samples were oven-dried at 80 °C till constant weight, and then nitrogen contents in plant tissues were determined by the Kjeldahl method. Grain yields were obtained from all plant harvest in field at maturity.

Data analysis

Total nitrogen accumulation was calculated as the sum of nitrogen accumulation in leaf blades, stems plus sheathes and panicles at maturity. PE was defined as grain production per unit nitrogen uptake by plants (Ladha et al., 1998). Single flag leaf nitrogen accumulation at heading was obtained from leaf dry weight and nitrogen content, the ratio of single leaf nitrogen accumulation to single leaf area was calculated and defined as leaf nitrogen content per unit area. Then ratios of Pn to nitrogen content per unit area in flag leaves were calculated, and defined as photosynthetic N-use efficiency (Pn/N). Nitrogen distribution ratio in leaf blades was quantified as the ratio of nitrogen accumulation in leaf blades to total nitrogen accumulation in plants. After calculations, correlation analyses were made between PE and Pn, Pn/N, nitrogen distribution ratio in leaf blades with SAS procedures (SAS, 1988).

Results

Grain yield, nitrogen accumulation and physiological N-use efficiency

Jinyou 253 harvested grain from 0.6759 kg m^{-2} to 0.7752 kg m^{-2} in the first season and 0.4564–

0.6256 kg m^{-2} in the second season. For Liangyoupeijiu and Baguixiang, the grain yields were 0.6949–0.7758 kg m^{-2} and 0.5726–0.6731 kg m^{-2} in the first season and 0.5910–0.6940 kg m^{-2} and 0.4720–0.6220 kg m^{-2} in the second season, respectively. Rice indicated higher grain yield at greater NA within the range of 0–15.7 g N m^{-2} regardless of genotypes and growing seasons. Under smaller NA (9.8 g N m^{-2}), rice obtained more grain at greater EFDR (2/3). However, under greater NA (15.7 g N m^{-2}), rice harvested more grain at smaller EFDR (1/3). The differences of grain yield between two NA and between two EFDR were not significant ($P > 0.05$) in both seasons (Table 1).

Jinyou 253 accumulated 8.435–14.220 g N m^{-2} in the first season and 5.116–11.526 g N m^{-2} in the second season. Liangyoupeijiu and Baguixiang accumulated 9.169–16.063 g N m^{-2} and 8.959–14.482 g N m^{-2} in first season, 6.563–13.564 g N m^{-2} and 6.210–12.497 g N m^{-2} in the second season, respectively. Nitrogen accumulation in three genotypes showed similar responsiveness to nitrogen supply. Compared among different NA treatments, rice indicated more nitrogen accumulation at greater NA. Under the same NA, rice plant accumulated more nitrogen at greater EFDR. The differences of nitrogen accumulation in the same genotype among nitrogen treatments were significant ($P < 0.05$) in both seasons (Table 1).

Physiological N-use efficiency (PE) in three genotypes ranged 42.12–80.14 g g^{-1} in the first season and 49.29–90.05 g g^{-1} in the second season, differing with genotypes, NA and EFDR. Unlike nitrogen accumulation, three genotypes indicated larger PE at smaller NA and at smaller EFDR under the same NA (Table 1).

Net photosynthetic rate (Pn) and photosynthetic N-use efficiency

Pn in flag leaves at heading varied with genotypes and nitrogen managements. Of three genotypes, Jinyou 253 presented significant ($P < 0.05$) higher Pn than Liangyoupeijiu and Baguixiang, and the difference of Pn between Liangyoupeijiu and Baguixiang was not significant ($P > 0.05$) in both growing seasons. Although the differences of Pn among nitrogen treatments in some cases were not significant,

Table 1. Grain yields, nitrogen accumulations and physiological N-use efficiencies (PE) in three rice genotypes under different nitrogen amounts (NA) and EFDR in the first and second season in 2002. Grain yield was the grain sun-dried weight from all plant harvest in field. EFDR was defined as the ratio of nitrogen fertilization given during ear development period to total NA. Nitrogen accumulation was quantified as the sum of nitrogen accumulation in leaves, stems + sheathes, and panicles at maturity, nitrogen was quantified by employing Kjeldahl's method with VAP50 (Gerhart, Germany). PE was defined as the ratio of grain yield to nitrogen accumulation in plants

Genotype	NA (g m ⁻²)	EFDR	Grain yield (kg m ⁻²)		N accumulation (g m ⁻²)		PE (g g ⁻¹)	
			First season	Second season	First season	Second season	First season	Second season
Jinyou253	0		0.6759	0.4564	8.435	5.116	80.14	89.13
	9.8	1/3	0.7502	0.5455	12.297	7.648	60.99	71.26
	9.8	2/3	0.7752	0.5520	13.918	8.373	55.68	65.93
	15.7	1/3	0.7621	0.6256	13.794	8.904	55.24	70.31
	15.7	2/3	0.7277	0.6185	14.220	115.26	51.20	53.62
Mean			7.38	5.59	125.33	83.13	60.65	70.05
Liangyoupeijiu	0		0.6949	0.5910	9.169	6.563	75.80	90.05
	9.8	1/3	0.7675	0.6244	11.886	10.407	64.53	59.96
	9.8	2/3	0.7709	0.6576	12.987	11.656	59.37	56.45
	15.7	1/3	0.7758	0.6940	13.704	12.039	56.63	57.65
	15.7	2/3	0.7664	0.6736	16.063	13.564	47.69	49.69
Mean			7.55	6.48	127.62	108.46	60.80	62.76
Baguixiang	0		0.5726	0.4720	8.959	6.210	63.96	76.01
	9.8	1/3	0.5565	0.5971	11.298	9.083	58.06	65.73
	9.8	2/3	0.6624	0.6042	11.611	9.385	57.01	64.36
	15.7	1/3	0.6731	0.6220	13.307	11.290	50.57	55.09
	15.7	2/3	0.6102	0.6155	14.482	12.497	42.12	49.29
Mean			6.35	5.82	119.31	96.93	54.35	62.10

three genotypes always showed higher Pn at greater NA and EFDR in spite of the growing seasons. Pn/N indicated contrary responsiveness to nitrogen supply. That is, when NA was considered, three genotypes presented greater Pn/N at lower NA, when EFDR was considered, three genotypes presented greater Pn/N at smaller EFDR. Compared among genotypes, Jinyou 253 showed significantly ($P < 0.05$) higher Pn/N than Liangyoupeijiu and Baguixiang (Table 2).

Nitrogen distribution in plants

Three rice genotypes distributed more than 40% nitrogen in leaf blades at heading and more than 10% at maturity in both growing seasons. Greater ratios of nitrogen in leaf blades were seen at heading and maturity under greater NA and EFDR in spite of genotypes and seasons. Compared among genotypes, Liangyoupeijiu at heading and Jinyou 253 at maturity distributed

the least nitrogen in leaf blades in both growing seasons, while Baguixiang distributed the most nitrogen in leaf blades in spite of growing stages and seasons.

Relationship of PE with Pn, Pn/N and nitrogen distribution in leaf blades

PE synthetically presented the ability of rice producing grain with absorbed nitrogen on the level of population. Similarly, Pn and Pn/N indicated the ability of rice producing matter and the efficiency of rice producing matter with nitrogen in flag leaves on the level of stoma, respectively. Theoretically, some relationship between PE and Pn, Pn/N would be existed. In this study, PE was not related to Pn in flag leaves at heading (Figure 1), but significantly ($P < 0.05$) related with Pn/N (Figure 2) in flag leaves at heading as reported by Wu and Tao (1995), Debabrata et al. (2003). PE also indicated significantly ($P < 0.05$) association with nitrogen distribution ratios in

Table 2. Photosynthetic rate (Pn) and photosynthetic N-use efficiency (Pn/N) in flag leaves at heading in three rice genotypes under different nitrogen managements in the first and second seasons in 2002. Pn – flag leaf photosynthetic rate at heading, measured with hand portable photosynthetic system (CID310, USA) at PPFD of $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$, leaf temperature of $30 \text{ }^\circ\text{C}$, mass flow of $0.3 \text{ mol m}^{-2} \text{ s}^{-1}$. Pn/N – flag leaf photosynthetic N-use efficiency at heading, defined as the ratio of Pn to nitrogen content per unit leaf area in flag leaf at heading, leaf area was measured with a Laser Area Meter (CI203, USA). EFDR was defined as the ratio of nitrogen fertilization given during ear development period to total NA

Genotype	NA (g m^{-2})	EFDR	Pn ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)		Pn/N ($\mu\text{mol CO}_2 \text{ g}^{-1} \text{ N s}^{-1}$)	
			First season	Second season	First season	Second season
Jinyou253	0		21.10	25.12	17.14	18.34
	9.8	1/3	21.98	25.70	15.51	18.09
	9.8	2/3	22.68	26.91	14.44	17.09
	15.7	1/3	22.06	25.70	14.67	17.32
	15.7	2/3	23.65	26.96	14.53	17.24
Mean			22.29	26.08	15.26	17.62
Liangyoupeijiu	0		18.25	20.17	14.93	17.61
	9.8	1/3	19.98	20.77	15.49	14.88
	9.8	2/3	20.61	21.22	14.71	14.67
	15.7	1/3	18.63	20.15	13.41	14.80
	15.7	2/3	19.68	22.53	13.16	14.76
Mean			19.43	20.97	14.34	15.34
Baguixiang	0		18.77	20.08	16.94	16.38
	9.8	1/3	19.87	20.17	14.82	15.66
	9.8	2/3	20.34	21.36	14.21	15.49
	15.7	1/3	19.35	21.41	15.12	15.99
	15.7	2/3	20.62	21.85	12.96	14.70
Mean			19.79	20.97	14.81	15.64

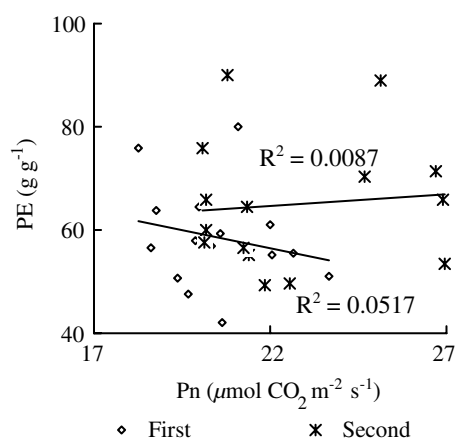


Figure 1. Relationship between physiological N-use efficiency (PE) and photosynthetic rate Pn in flag leaves at heading in the first and second seasons. PE was defined as grain production per unit nitrogen uptake by plants, grain yield was the grain sun-dried weight from all plant harvest in field, nitrogen contents in plant tissues were determined with a VAP50 Kjeldahlmeter (Gerhart, Germany). Pn in flag leaves were measured in field with a portable photosynthetic system (CID310, USA) at PPFD of $1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$, leaf temperature of $30 \text{ }^\circ\text{C}$, mass flow of $0.3 \text{ mol m}^{-2} \text{ s}^{-1}$

leaf blades at heading and maturity in both growing seasons except at heading in early season (Figure 3). Results suggested that low PE in rice genotypes under great NA and heavy ear fertilization is associated to more nitrogen distribution in leaf blades and decreases in photosynthetic efficiency.

Discussion

Nitrogen fertilizer is one of the most important agronomic inputs and limiting factors for realizing the potential grain production in developing countries. Therefore, nitrogen strategy has been well documented in many literatures. When nitrogen strategy is involved, grain production and PE are two major factors considered. However, grain production and PE in some cases showed different responsiveness to nitrogen strategy. In our results, three genotypes presented higher grain production at 1/3 of EFDR under

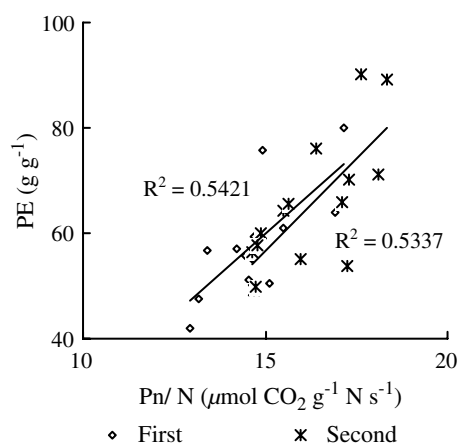


Figure 2. Relationship between physiological N-use efficiency (PE) and photosynthetic N-use efficiency (Pn/N) in flag leaves at heading in the first and second seasons. PE was defined as grain production per unit nitrogen uptake by plants, grain yield was the grain sun-dried weight from all plant harvest in field, nitrogen contents in plant tissues were determined with a VAP50 Kjeldahmeter (Gerhart, Germany). Pn in flag leaves were measured in field with a portable photosynthetic system (CID310, USA) at PPFD of $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$, leaf temperature of $30 \text{ }^\circ\text{C}$, mass flow of $0.3 \text{ mol m}^{-2} \text{s}^{-1}$. Photosynthetic N-use efficiencies in flag leaves were calculated as ratios of Pn to nitrogen content per unit area in flag leaves

greater NA, or at 2/3 under smaller NA, yet PE at 2/3 of EFDR were lower than those at 1/3 of EFDR in spite of NA (Table 1).

Nitrogen accumulation and grain production are two different and correlative physiological

processes in rice plant. It has been reported that 53% of nitrogen applied at panicle initiation was absorbed by rice plant within 10 days (Cassman et al., 1998), and maximum nitrogen uptake rates of $0.9\text{--}1.2 \text{ g m}^{-2} \text{ d}^{-1}$ were observed over the 4-d period following nitrogen application (Peng and Cassman, 1998). These observations suggested that nitrogen uptake was a relative simple process and most fertilizer-N uptake by rice plant was finished within a quite short time at a quite rapid speed, therefore three genotypes indicated higher nitrogen accumulation under greater NA and EFDR (Table 1). However, grain yield is the integrated results of events occurring throughout growth and development of the plant and determined by various factors related to the plant and the environment. Therefore, grain production is a much more complicated physiological process than nitrogen accumulation, increase in nitrogen accumulation would not always resulted in proportioned increase in grain production. This may explain why nitrogen accumulation and grain production sometimes indicated different responsiveness to nitrogen supply.

Nitrogen in plants occurred in different forms, some are related to photosynthesis, the others are not. Rubisco is one of the most important kinds of nitrogenous compounds in leaves related to photosynthesis. Rubisco was accounted for above 25% of total nitrogen and above 50% soluble nitrogen in leaves (Makino et al., 1984) and usually became

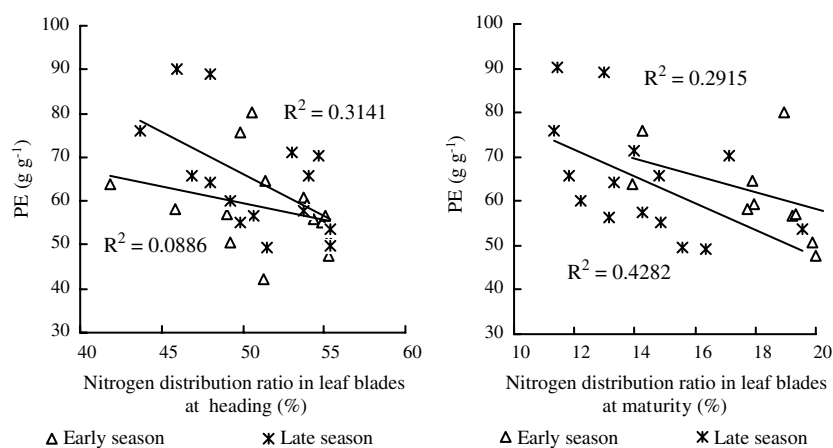


Figure 3. Relationships of physiological N-use efficiency (PE) with nitrogen distribution ratios in leaf blades at heading and maturity in the first and second seasons in 2002. PE was defined as grain production per unit nitrogen uptake by plants, grain yield was the grain sun-dried weight from all plant harvest in field, nitrogen contents in plant tissues were determined with a VAP50 Kjeldahmeter (Gerhart, Germany). Nitrogen distribution ratios were calculated as nitrogen accumulation in leaf blades to total nitrogen accumulation in plants.

Table 3. Nitrogen distribution in plants of three rice genotypes at heading and maturity in the first and second seasons in 2002. Four representative hills of plants based on field investigation were separately sampled and divided into leaf blades, stems + sheathes, panicles. Nitrogen contents in plant tissues were determined by the Kjeldahl method. Nitrogen distribution ratios in plant tissues were quantified as the ratios of nitrogen accumulation in the tissue to total nitrogen accumulation in plants

Genotype	NA (g m ⁻²)	EFDR	Heading			Maturity		
			Stem + sheath (%)	Leaf blade (%)	Panicle (%)	Stem + sheath (%)	Leaf blade (%)	Panicle (%)
First season								
Baguixiang	0		31.26	50.58	18.16	14.52	18.93	66.55
	9.8	1/3	31.02	53.78	15.20	14.03	22.52	63.45
	9.8	2/3	30.15	54.38	15.47	13.91	22.54	63.55
	15.7	1/3	32.00	54.85	13.15	14.84	23.35	61.81
	15.7	2/3	30.40	55.33	14.27	15.43	24.51	60.06
Jinyou 253	0		32.27	49.89	17.84	12.08	14.24	73.68
	9.8	1/3	31.01	51.43	17.56	15.00	17.91	67.09
	9.8	2/3	30.93	53.9	15.17	14.38	17.94	67.68
	15.7	1/3	30.52	55.12	14.36	13.96	19.25	66.79
	15.7	2/3	30.82	55.31	13.87	14.58	20.01	65.41
Liangyoupeijiu	0		37.32	41.86	20.82	14.44	13.94	71.62
	9.8	1/3	34.97	45.86	19.17	15.62	17.72	66.66
	9.8	2/3	35.26	49.06	15.68	15.42	19.36	65.22
	15.7	1/3	35.22	49.25	15.53	16.83	19.91	63.26
	15.7	2/3	35.43	51.27	13.30	17.47	26.52	56.01
Second season								
Baguixiang	0		34.52	47.98	17.50	19.34	12.99	67.67
	9.8	1/3	33.09	53.07	13.84	20.36	14.00	65.64
	9.8	2/3	33.17	54.01	12.82	20.52	14.78	64.70
	15.7	1/3	31.63	54.64	13.73	22.96	17.14	59.90
	15.7	2/3	33.61	55.39	11.00	22.10	19.54	58.36
Jinyou 253	0		35.79	45.98	18.23	19.50	11.43	69.07
	9.8	1/3	33.32	49.19	17.49	18.27	12.21	69.52
	9.8	2/3	33.06	50.66	16.28	18.70	13.13	68.17
	15.7	1/3	31.67	53.73	14.60	18.08	14.23	67.69
	15.7	2/3	30.55	55.42	14.03	19.79	15.58	64.63
Liangyoupeijiu	0		36.11	43.72	20.17	17.79	11.31	70.90
	9.8	1/3	35.78	46.86	17.36	19.27	11.83	68.90
	9.8	2/3	34.84	48.05	17.11	18.72	13.31	67.97
	15.7	1/3	35.75	49.87	14.38	21.07	14.85	64.08
	15.7	2/3	36.06	51.46	12.48	20.90	16.38	62.72

the limiting factors to photosynthesis under enough light (Makino et al., 1983). However, Rubisco content in rice plants was 30–40% lower than those of other C₃ plants such as wheat (Evans and Austin, 1986; Makino et al., 1988), and its proportion to leaf nitrogen have remained almost unchanged regardless of rice breeding which maybe explain why rice breeding have not resulted in the enhancement of leaf photosynthesis (Mae,

1997). In our study, we did not measure Rubisco content in flag leaves, but determined total protein-N content in flag leaves. Results showed that total protein-N content increased with increase of NA and EFDR, yet its proportion to leaf nitrogen presented little responsiveness to nitrogen supply (data are not republished). However, nitrogen distribution in leaf blades shifted with nitrogen management. Under greater NA and EFDR, rice

plants distributed more nitrogen in leaf blades in spite of genotypes and seasons (Table 3). From these observations, we suppose that more nitrogen distribution in leaf blades and little change in proportion of Rubisco to leaf nitrogen under greater NR and EFDR resulted in decrease in Pn/N, and decrease in Pn/N resulted in decrease in PE.

Acknowledgements

We thank professors Weixing Cao, Tingbo Dai and Dong Jiang in Nanjing Agricultural University for their generous assistance. The field study was conducted in Agricultural Experiment Station of Guangxi University, Nanning, China, and physiological measurements were carried out at Key Laboratory of Crop Cultivation and Farming System of Guangxi Province, Guangxi University, Nanning, China. Research funds were from Education Department of Guangxi Province (2002316) and Guangxi University, Nanning, China.

References

- Broadbent F E, De Datta S K, Laureles E V 1987 Measurement of nitrogen utilization efficiency in rice genotypes. *Agron. J.* 79, 786–791.
- Cassman K G, Peng S, Olk D C, Ladha J K, Reichardt W, Dobermann A, Singh U 1998. Opportunities for increased nitrogen-use efficiency from improved resource management in irrigated rice systems. *Field Crops Res.* 56, 7–39.
- De Datta S K and Broadbent F E 1990 Nitrogen-use efficiency of 24 rice genotypes on an N-deficient soil. *Field Crops Res.* 23, 81–92.
- De Datta S K and Broadbent F E 1993 Development changes related to nitrogen-use efficiency in rice. *Field Crops Res.* 34, 47–56.
- Debabrata R, Sheshshayee M S, Mukhopadhyay K, Bindumadhava H, Prasad T G, Udaya K M 2003 High nitrogen use efficiency in rice genotypes is associated with higher net photosynthetic rate at lower Rubisco content. *Biol. Plant* 46, 251–256.
- Evans J R and Austin R B 1986 The specific activity of ribulose-1,5-bisphosphate carboxylase in relation to genotype in wheat. *Planta* 167, 344–350.
- Fisher K S 1998 Toward increasing nutrient-use efficiency in rice cropping systems: The next generation of technology. *Field Crops Res.* 56, 1–6.
- Jiang L G, Dai T B, Wei S Q, Gan X Q, Xu J Y, Cao W X 2003 Genotypic differences and evaluation in nitrogen uptake and utilization efficiency in rice. *Acta Phytoecol. Sin.* 27, 466–471.
- Jiang L G, Cao W X, Gan X Q, Xu J Y, Dong D F, Chen N P, Lu F Y, Qin H D 2004 Nitrogen uptake and utilization under different nitrogen management and influence on grain yield and quality in rice. *Agri. Sci. China* 37(4), 490–496.
- Ladha J K, Kirk G J D, Bennett J, Peng S, Reddy C K, Reddy P M, Singh U 1998 Opportunities for increased nitrogen-use efficiency from improved lowland rice germplasm. *Field Crops Res.* 56, 41–71.
- Lin Q H 2000 *Crop Population Quality*. Shanghai Science & Technology Press, Shanghai. pp. 96–107 (in Chinese with English abstract).
- Mae T 1977 Physiological nitrogen efficiency in rice: nitrogen utilization, photosynthesis, and yield potential. *Plant Soil* 196, 201–210.
- Makino A, Mae T, Ohira K 1983 Photosynthesis and ribulose 1,5-bisphosphate carboxylase in rice leaves. *Plant Physiol.* 73, 1002–1007.
- Makino A, Mae T, Ohira K 1984 Relation between nitrogen and 1,5-bisphosphate carboxylase in rice leaves from emergence through senescence. *Plant Cell Physiol.* 25, 429–437.
- Makino A, Mae T, Ohira K 1988 Differences between wheat and rice in the enzymic properties of ribulose-1,5-bisphosphate carboxylase/oxygenase and the relationship to photosynthetic gas exchange. *Planta* 174, 30–38.
- Ohnishi M, Horie T, Homma K 1999 Nitrogen management and cultivar effects on rice yield and nitrogen use efficiency in Northeast Thailand. *Field Crops Res.* 64, 109–120.
- Peng S and Cassman K G 1998 Upper thresholds of nitrogen uptake rates and associated nitrogen fertilizer efficiencies in irrigated rice. *Agron. J.* 90, 178–185.
- Peng S, Garcia F V, Laza R C, Sanico A L, Samson M L 1996a Nitrogen use efficiency of irrigated tropical rice established by broadcast wetseeding and transplanting. *Fert. Res.* 45, 123–134.
- Peng S, Garcia F V, Laza R C, Sanico A L, Visperas R M, Cassman K G 1996b Increased N-use efficiency using a chlorophyll meter on high-yielding irrigated rice. *Field Crops Res.* 47, 243–252.
- SAS Institute 1998 *SAS/STAT user's guide*. Release 6.03. SAS Institute, Cary. NC.
- Wu P and Tao Q N 1995 Genotypic response and selection pressure on nitrogen-use efficiency in rice under different nitrogen regimes. *J. Plant Nutr.* 18, 487–500.

Section editor: H. Lambers