Intraspecific variation in photosynthetic nitrogen-use efficiency is positively related to photosynthetic rate in rice (Oryza sativa L.) plants

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Abstract

To explore the natural variation in leaf photosynthesis and investigate its relations with leaf nitrogen (N) status, 121 rice cultivars were pot-grown and their leaf photosynthetic rate ($P_N$) and N content were measured on the flag leaves at heading stage before anthesis. The results showed that there were substantial natural variations in $P_N$, leaf N content based on leaf area and leaf mass, and photosynthetic N-use efficiency (PNUE). $P_N$ ranged between 15.4 and 32.6 μmol m$^{-2}$ s$^{-1}$; $P_N$ and PNUE of four widely grown cultivars in China were significantly lower than $P_N$ and PNUE of the cultivar Nancay PA, which possessed the highest values for $P_N$ and PNUE. Moreover, PNUE was positively related to $P_N$ across cultivars, the high PNUE was related to high stomatal conductance, high transpiration, and low leaf mass per area. We concluded that intraspecific variation in PNUE is positively related to $P_N$ in rice plants.

Additional key words: CO$_2$ diffusion conductance; leaf anatomy; leaf hydraulic conductance.

Introduction

Improvements in crop management and genetic gain in harvest index lead to a dramatic increase in crop yields, which have more than doubled since 1960 (Long et al. 2015). Although the yields continue to increase in most growing areas on a global scale, the yield improvements are stagnating or even moving in reverse at about 24–39% of the growing areas for maize, rice, wheat, and soybean crops (Ray et al. 2012, Long 2014). Ray et al. (2013) found that the global yields of these four major crops are now increasing at a rate of 1.6, 1.0, 0.9, and 1.3% per year, respectively, which is far less than the rate of 2.4% per year required to double global production by 2050. Therefore, a second Green Revolution is needed to boost crop production and to meet the rising demand.

Over the past 50 years, intercepted radiation and the harvest index have been largely improved, but the conversion efficiency of visible solar energy, which is related to photosynthesis and respiratory loss, has not been improved (Long et al. 2015). Thus, increasing energy conversion efficiency can promote the yield.

Many researches have aimed to select genotypes for high photosynthesis and were successful in identifying such cultivars (Moss and Musgrave 1971, Austin et al. 1982, Shibles et al. 1987), but most of these cultivars could not reach the higher crop yield (Moss and Musgrave 1971, Ford et al. 1983). The main reason is the complexity of relations between instantaneous assimilation rate of a single leaf and the biomass/yield at the level of a crop canopy. The yield formation is a complex process, the relationship between yield and photosynthesis of a single leaf may be influenced by many factors, such as respiration rate, transportation, etc. In addition, Sinclair et al. (2004) illustrated that the impact of factors that underlie crop yield can be diminished when scaling up to a higher level, e.g., a 50% increase in mRNA synthesis for Rubisco carboxylase finally increases (or even decreases) yield by up to 6% depending on the level of nitrogen accumulation. Therefore, though many previous researches showed weak relations between the yield and net photosynthetic rate ($P_N$), improving $P_N$ and ascertaining its mechanism is necessary for future breeding work.

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Abbreviations: $E$ – leaf transpiration rate; EFM – evaporative flux method; $f_{ic}$ – fraction of intercellular air space; $g_C$ – mesophyll conductance to CO$_2$; $g_s$ – stomatal conductance to H$_2$O; HPFM – high pressure flowmeter method; $K_{hi}$ – leaf hydraulic conductance; $K_{hi}$ – leaf hydraulic conductance inside xylem; LES – leaf economic spectrum; LMA – leaf mass per area; $N_{N}$ – leaf nitrogen content based on leaf area; $N_{N}$ – leaf nitrogen content based on leaf mass; $P_N$ – net photosynthetic rate; PNUE – photosynthetic nitrogen-use efficiency; RKM – rehydration kinetics method; $S_i$ – surface area of chloroplasts exposed to intercellular airspaces per leaf area; $S_{nc}$ – mesophyll cell wall surface area exposed to intercellular airspace per leaf area; SSNM – site-specific nitrogen management; VPM – vacuum pump method.

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There are many approaches to enhance $P_N$, for example, designing more efficient Rubisco, increasing mesophyll conductance ($g_m$), and introducing the C$_4$ photosynthetic pathway into C$_3$ crops (Long et al. 2006). Suzuki et al. (2007) have increased the Rubisco content in rice leaves using transgenic methods, but it failed to enhance $P_N$ due to the changes in N distribution. Introduction of C$_4$ photosynthetic pathway into C$_3$ crops seems to be an attractive and promising way to increase $P_N$, however, it can take several decades to achieve this ambitious aim due to difficulties in changing leaf anatomy (as C$_4$ plants have special Kranz anatomy) and the complex biochemical actions. Therefore, other strategies should be considered to increase $P_N$ at present.

In addition to these genetic approaches, exploiting natural variation in leaf photosynthesis can also contribute to increasing crop productivity, e.g., rice production (Gu et al. 2014). Using the crop model GECROS (Yin and van Laar 2005), Gu et al. (2014) showed that improving $P_N$ by exploiting its genetic variation in rice plants can effectively increase biomass production, it shows that an increase in $P_N$ by 25% can lead to an increase in biomass production of 22–29%. Natural genetic variation is the fuel of evolution, and is a prerequisite for natural or artificial selection (Flood et al. 2011). However, the natural variation in crop photosynthesis has not been fully studied and exploited, as most studies on photosynthesis are conducted with a few varieties (Cook and Evans 1983, Sasaki and Ishii 1992, Yeo 1994, Giuliani et al. 2011). However, the experiments with 121 rice cultivars, using 121 rice cultivars.

Materials and methods

Plant materials and N input: A total of 121 rice cultivars were collected from 13 countries (Table 1S, supplement). After germination on moist filters on 11 May 2014, rice cultivars were transferred to nursery plates. When the seedlings developed in average of three leaves, they were transplanted to 11-L pots with a density of three hills per pot and two seedlings per hill. There were five pots per cultivar and each pot was filled with 10 kg of soil, phosphorus (P) and potassium (K) were applied as basal fertilizers at an amount of 1.5 g per pot. N was applied at the amount of 2 g(N) per pot, 40% of which was applied as a basal fertilizer and next two topdressings of 30% each were applied at mid-tillering and the heading stages, respectively. Plants were watered daily, and a minimum 2-cm water layer was maintained to avoid drought stress. Pests were intensively controlled using chemical pesticides. The experiment was
conducted outdoors in Huazhong Agricultural University (114.37°E, 30.48°N) in Wuhan City, Hubei Province, China. Measurements were conducted at the heading stage before anthesis.

**Gas exchange** was measured with a portable photosynthesis system (LI-6400XT, LI-COR Inc., Lincoln, NE, USA) on the flag leaves between 09:00 and 16:00 h. Throughout all experiments, PPFD during measurements was set to 1,500 μmol(photons) m⁻² s⁻¹ using a red-blue LED artificial light source, with 10% of blue light. Relative humidity was controlled at ~60% to minimize the impacts of environmental conditions, with 10% of blue light. Relative humidity was kept constant at ~60% to minimize the impacts of environmental conditions, with 10% of blue light. Leaf temperature was set to 28°C. Data were recorded after equilibration to a steady state, about 20 min after enclosing the leaves in the leaf chamber.

In order to compare photosynthetic characteristics of leaves with a similar developmental age, gas-exchange measurements of each cultivar were conducted immediately after the flag leaves fully expanded. The measurements lasted for 19 d in July and August, and 5–6 cultivars were typically examined in a single day. The measurements were conducted only on sunny days, during which the radiation intensity, average temperature, and relative humidity were 19.2 ± 4.6 MJ m⁻² d⁻¹, 29.1 ± 2.4°C, and 77.0 ± 5.8%, respectively (Fig. 3, supplement). Moreover, the environmental conditions in the leaf chamber were tightly controlled by the gas-exchange instrument, which minimized the variations of gas-exchange parameters caused by different ambient environmental conditions. To minimize the diurnal variation of photosynthesis, the measurements were suspended when significant midday depression occurred.

**Leaf N content measurements**: Leaves were detached immediately after the gas-exchange measurements, followed by leaf area measurement using a LI-Cor 3000C leaf area analyzer. Leaves were then oven-dried at 80°C until they achieved a constant mass. Afterwards, leaf dry mass was weighed, and leaf mass per area was calculated as the ratio of leaf dry mass to leaf area. Mass-based leaf photosynthesis (Pmass, μmol g⁻¹ s⁻¹) was calculated using the equation:

\[
P_{\text{mass}} = \frac{P_{N}}{\text{LMA}}
\]  

(1)

**Leaf equation**: Leaf N content based on leaf mass (Nmass) was measured with an Elementar Vario MAX CN analyzer (Elementar Analysensysteme GmbH, Hanau, Germany), and Nmass was calculated by multiplying Nmass with LMA. PNUE was calculated using the equation:

\[
\text{PNUE} = \frac{P_{N}}{N_{\text{area}}}
\]  

(2)

**Statistical analysis**: One-way analysis of variance (ANOVA) was used to assess varietal differences in each parameter using Statistix 9 software (Analytical Software, Tallahassee, Florida, USA). Linear regression analysis was performed to test the correlations between parameters using SigmaPlot 10 (Systat Software Inc., California, USA). The normal distribution tests of the various photosynthesis traits were conducted by One-sample Kolmogorov-Smirnov’s test using SPSS 16.0 (SPSS Inc., Chicago, IL, USA).

**Results**

Narea and Nmass showed great variations among 121 rice cultivars (Fig. 1, Table 1S). Narea ranged from 0.94 g m⁻² for cultivar N22 (NO. 108) to 1.99 g m⁻² for cultivar Belgioioso (NO. 54), with a mean value of 1.51 g m⁻². Nmass ranged from 1.70% for cultivar Yangdao 6 (NO. 144) to 3.83% for cultivar PI 282203 (NO. 88), with a mean value of 2.78%. Similarly, Pmass was highly variable among the 121 rice cultivars, ranged from 15.5 μmol m⁻² s⁻¹ for cultivar N22 (NO. 108) to 32.6 μmol m⁻² s⁻¹ for cultivar Nancay PA (NO. 33), with a mean value of 23.3 μmol m⁻² s⁻¹ (Fig. 2A, Table 1S). Differences between cultivars were highly significant. Narea of the cultivar with the highest Pmass (cultivar 33, Nancay PA) was 1.45 g m⁻² (Nmass = 2.39%; Fig. 1, Table 1S), which was lower than the mean value of 1.51 g m⁻² (2.78% for Nmass). Pmass of widely grown rice cultivars in China – Huanghuazhan (NO. 99), Shanyou 63 (NO. 110), Liangyoupeijiu (NO. 107), and Yangliangyou 6 (NO. 118) – were 23.6, 25.0, 25.7, and 26.1 μmol m⁻² s⁻¹, respectively (Fig. 2, Table 1S). These values were slightly (1.3–12.0%) higher than the mean value of all the 121 cultivars, but were significantly lower (19.9–27.8%) than the highest Pmass (32.6 μmol m⁻² s⁻¹). Narea of these four cultivars were 1.55, 1.56, 1.65, and 1.69 g m⁻², which were 2.6–11.9% higher than the mean Narea of all the cultivars and were 7.9–17.1% higher than cultivar 33 (Fig. 1, Table 1S). Nmass were 2.44, 2.59, 2.99, and 2.91%, respectively, which were either lower (for cultivars 99 and 107) or higher (for cultivars 110 and 118) than the mean value of 2.78% in all cultivars. But they were all higher (2.2–24.9%) than that of the cultivar 33.

Across all cultivars, Pmass was positively related to Narea (Fig. 3A), but the correlation coefficient was very low (R² = 0.18). Narea of 1.4 g m⁻² is usually used as a threshold, below which N fertilization is needed in rice plants (Peng et al. 1996). If the correlation between Pmass and Narea was calculated for cultivars with Narea > 1.4 g m⁻², no significant correlation was observed (P = 0.1955, n = 91), while it was significant for cultivars with Narea < 1.4 g m⁻² (P = 0.003, n = 30). This suggested variation in Pmass when Narea > 1.4 g m⁻² did not result from differences in Narea (Table 1).

PNUE was also significantly different between all rice cultivars and ranged from 10.03 μmol(CO₂) g⁻¹(N) s⁻¹ for cultivar Banata 35 (NO. 43) to 22.57 μmol(CO₂) g⁻¹(N) s⁻¹ for cultivar Nancay PA (NO. 33) (Fig. 2B). PNUE was negatively related to Narea across all cultivars (Fig. 3B). Interestingly, PNUE was positively related to Pmass across all cultivars (Fig. 4), and Nancay PA possessed the highest Pmass and PNUE among all cultivars. This suggested that PNUE and Pmass can be simultaneously improved by
exploiting the natural variation of rice plants at the leaf scale. In comparison, PNUE of the widely grown cultivars 99, 107, 110, and 118 were 29.0–32.8% lower than that of the cultivar 33.

$g_s$ and $E$ also showed significant varietal differences between all rice cultivars. $g_s$ ranged from 0.22 mol(H$_2$O) m$^{-2}$ s$^{-1}$ for Elba (NO. 60) to 0.93 mol(H$_2$O) m$^{-2}$ s$^{-1}$ for Belgioioso (NO. 54), while $E$ ranged from 3.09 mmol (H$_2$O) m$^{-2}$ s$^{-1}$ for Ejingyou 775 (NO. 91) to 13.05 mmol (H$_2$O) m$^{-2}$ s$^{-1}$ for Baek Na (NO. 22). $P_N$ and $E$ both showed significant and positive relationships with $g_s$ (Fig. 5). In addition, PNUE showed positive relationships with both
NITROGEN-USE EFFICIENCY AND PHOTOSYNTHESIS CAN BE SIMULTANEOUSLY IMPROVED

LMA and $P_{\text{mass}}$ also showed significant differences between all rice cultivars (Supplementary Table 1S). LMA ranged from 38.10 g m$^{-2}$ for N22 (NO. 108) to 73.30 g m$^{-2}$ for Yongyou 12 (NO. 119), while $P_{\text{mass}}$ ranged from 0.27 μmol g$^{-1}$ s$^{-1}$ for Yangjing 4227 (NO. 115) to 0.70 μmol g$^{-1}$ s$^{-1}$ for Kirmizi Celtik (NO. 68). Moreover, $N_{\text{area}}$ was positively related to LMA, and PNUE was negatively related to LMA (Fig. 7).

$N_{\text{area}}$, $N_{\text{mass}}$, $P_{\text{N}}$, PNUE, $g_s$, $E$, LMA, and $P_{\text{mass}}$ were all normally distributed (Fig. 1S, supplement). There were

83 rice cultivars possessing $N_{\text{mass}}$ of 2.25–3.0% (68.6% of all cultivars), while 54 rice cultivars showed $N_{\text{area}}$ of 1.4–1.6 g m$^{-2}$ (44.6% of all cultivars). $P_{\text{N}}$ for 80 rice cultivars (accounting for 66.1% of all cultivars) ranged between 20–27 μmol m$^{-2}$ s$^{-1}$, while PNUE of 86 rice cultivars ranged between 13.0–18.0 μmol g$^{-1}$ (N) s$^{-1}$. There were only five cultivars whose $P_{\text{N}}$ was more than 30 μmol m$^{-2}$ s$^{-1}$.

Discussion

In the present study, 121 rice cultivars selected from worldwide were used to investigate the natural variation of leaf photosynthesis. PPFD of 1,500 μmol(photon) m$^{-2}$ s$^{-1}$ is a saturating light intensity for rice species according to previous studies (Li et al. 2009, Xiong et al. 2015, 2016, 2017), and is also a typical light intensity in midday during rice growth season at the experimental site. Therefore, this light intensity was used to study the intra-specific variation of photosynthesis in rice species.

The results showed that there was a large natural variation in leaf photosynthesis, ranging from 15.5 to 32.6 μmol m$^{-2}$ s$^{-1}$. The natural variation in leaf photosynthesis would potentially be larger if more cultivars were selected, especially, when including wild species with photosynthetic rates that range from 14.3 μmol m$^{-2}$ s$^{-1}$ for *Oryza glumaepatula* to 37.6 μmol m$^{-2}$ s$^{-1}$ for *Oryza rufipogon* (Zhao et al. 2010).

The yield improvement of the Green Revolution has been achieved largely through improved genetics, better crop management, and protection. Many studies during the period 1970–1980 have selected cultivars with higher photosynthetic rates to improve crop yield (Moss and Musgrave 1971, Ford et al. 1983). In present study, $P_{\text{N}}$ was not related to the year of cultivar release.
M. YE et al. (Fig. 2S, supplement). PN of widely grown cultivars, i.e., Huanghuazhan (NO. 99), Liangyoupeijiu (NO. 107), Shanyou 63 (NO. 110), and Yangliangyou 6 (NO. 118) in China, was only slightly (1.3–12.0%) higher than the mean value of all the 121 cultivars. By contrast, PN of the cultivar 33 was 24.9–38.1% higher than these widely grown cultivars. As we know, widely grown cultivars are widely planted mainly for their high grain yield and strong resistance to stresses. It means that relying on moderate photosynthetic rate can even reach a high yield level in these widely grown cultivars. If kept their advantages in other traits and improve their PN to 32.6 µmol m⁻² s⁻¹ (NO. 33’s level) by breeding, their yield might be further increased.

Intensive crop management strategies, such as site-specific nitrogen management (SSNM) and integrated soil-crop system management, have been developed to realize high-yield crops and high-efficiency production systems. In SSNM, N application is based on leaf N status measured with a chlorophyll meter or leaf color chart (Peng et al. 2010). According to this system, N is needed to be applied when N₉₀ of the topmost fully expanded leaf is lower than 1.4 g m⁻² (Peng et al. 1996). In the present study, N₉₀ showed a large variation from 0.94 to 1.99 g m⁻² among the tested cultivars, and N₉₀ in 91 out of 121 rice cultivars (accounting for 75.2%) was higher than this threshold (Table 1S). But it should be noted that N₉₀ in pot experiments is related to pot size and plant biomass (Poorter et al. 2012), and cultivars with high biomass accumulation are more limited by N supply. Further research should be conducted to investigate the response of photosynthesis to N supplies in these cultivars.

In the present study, N₉₀ of 1.4 g m⁻² was enough for some cultivars to achieve a high PN of about 30 µmol m⁻² s⁻¹, i.e., cultivar 33 and 38 achieved very high photosynthetic rates of 32.6 and 29.7 µmol m⁻² s⁻¹, with N₉₀ of 1.45 and 1.40 g m⁻², respectively. This suggested that improving photosynthesis in rice plants did not necessarily require more N input at the leaf scale. PNUE and PN was found to be positively related, which is an interesting finding. If PNUE and PN of widely grown cultivars can be improved to the level of the cultivar 33 through a conventional breeding approach, we can potentially produce more rice grains with less N input.

In addition to leaf N content, CO₂ diffusion conductance is one of the limiting factors to PN under current ambient conditions, and gₛ is highly correlated with plant hydraulic status and E. In present study, PN, E, and PNUE showed significant relationships with gₛ, and PNUE was also positively related to E. This suggested that high hydraulic transport efficiency enhances the stomatal CO₂ diffusion, and finally contributes to a high PNUE. Giuliani et al. (2013) illustrated that there was a coordination between photosynthesis, transpiration, and structural traits in rice and wild relatives. Xiong et al. (2017) have divided Kᵣ into two parts—leaf hydraulic conductance inside xylem (Kᵢ) and Kᵣ to investigate the effects of leaf morphological and anatomical traits on leaf hydraulic conductances and CO₂ diffusion conductance. And they suggested that the relationship between Ke and gₛ is coordinated by leaf anatomy, including the fraction of intercellular airspace (fᵢ), mesophyll cell wall thickness, mesophyll cell wall surface area exposed to intercellular airspace per leaf area (Sᵢᵢ), and surface area of chloroplasts.

Fig. 6. Correlations of photosynthetic nitrogen-use efficiency (PNUE) with stomatal conductance (gₛ) and transpiration rate (E) across 121 rice cultivars.
exposed to intercellular airspace (S). However, there are some problems for Kx and Kox because they are difficult to be directly and accurately measured, although several approaches (including the evaporative flux method (EFM), the rehydration kinetics method (RKRM), the high pressure flowmeter method (HPFM), and the vacuum pump method (VPM)) for determining Kwm have been developed (Flexas et al. 2013, Xiong et al. 2017). After diffusing out of leaf veins in liquid phase, water should evaporate through existing stomata as water vapor (Rockwell et al. 2014). Where does the evaporation occur is unknown, although Rockwell et al. (2014) reported that it mainly occurred at the vascular bundles and peristomal regions in red oak (Quercus rubra) trees. Moreover, environmental variations may have some impact on Kwm. Environmental conditions surrounding leaves can effectively influence the liquid and vapor phases in the outside-xylem regions. For example, Buckley et al. (2015) predicted that vapor-phase can contribute up to 39.2–44% of Kwm when temperature gradient between vascular plain and the epidermis is 0.2 K. It suggested that temperature can strongly affect the liquid and vapor status inside leaves. Therefore, it is necessary to develop direct and more accurate methods for Kx and Kwm measurements, and to study their responses to environmental changes, such as temperature and light intensity.

LMA is an important leaf structural trait, which can substantially affect leaf photosynthesis and plant growth. The dry mass of a leaf consists of a wide range of components, which can be divided into eight different classes, including structural carbohydrates, lignin, and minerals among others (Poorter et al. 2009). As one of the most important minerals, N content per leaf area was thus observed to be increased in high-LMA leaves (Hikosaka and Shigeno 2009), and a similar result was observed in present study (Fig. 7A). Moreover, PNUE was shown to be negatively related to LMA (Fig. 7B), which was consistent with previous studies (Takashima et al. 2004, Hikosaka and Shigeno 2009). This suggested that leaf anatomy can substantially affect leaf photosynthesis and PNUE. For mesophyll diffusion pathway, after diffusing through stomata, CO2 needs to pass through the cell wall, cell membrane, cytoplasm, chloroplast envelope, and stroma to reach carboxylation sites. Thus, gs, is greatly determined by leaf anatomy, such as the fraction of intercellular air space (fwa), Ss, Sc, and cell wall thickness (Evans et al. 2009, Scafaro et al. 2011, Terashima et al. 2011, Peguero-Pina et al. 2012, Tosens et al. 2012, Giuliani et al. 2013, Tomás et al. 2013, Muir et al. 2014). Generally, leaves possessing the high LMA usually have thicker cell wall, smaller intercellular air spaces (low fwa, Sc, Ss) and relatively lower gs, and PNUE (Terashima et al. 2006, Tosens et al. 2012, Onoda et al. 2017). In addition, leaves possessing different LMA also have different N distribution. Onoda et al. (2017) have investigated physiological and structural tradeoffs underlying the leaf economics spectrum (LES) by analyzing a novel data compilation. It demonstrated that leaves with the high LMA, and a greater fraction of leaf dry mass in cell wall typically have a lower fraction of N in photosynthetic proteins, and thus low CO2-diffusion rates. More research should be conducted to explore the N allocation in leaves with different LMA and its effects on PNUE.

**Conclusions:** The current study revealed that there are substantial natural variations in Pn, Narea, Nmass, and PNUE, and a large potential still exists to improve Pn and PNUE in widely grown rice cultivars. Pn and PNUE for four widely grown rice cultivars were 19.9–27.8% and 29.0–32.8% lower than the cultivar 33 (Nancay PA), Narea of 1.4 g m\(^{-2}\) was enough for some cultivars to achieve high photosynthesis of 30 μmol m\(^{-2}\) s\(^{-1}\). PNUE showed a positive relationship with Pn across the 121 rice cultivars, and the high PNUE was associated with the high gs, E, and low LMA.

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