Leaf photosynthetic parameters related to biomass accumulation in a global rice diversity survey

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Abstract

Mining natural variations is a major approach to identify new options to improve crop light use efficiency. So far, successes in identifying photosynthetic parameters positively related to crop biomass accumulation through this approach are scarce possibly due to the earlier emphasis on properties related to leaf instead of canopy photosynthetic efficiency. This study aims to uncover rice natural variations to identify leaf physiological parameters that are highly correlated with biomass accumulation, a surrogate of canopy photosynthesis. To do this, we systematically investigated 14 photosynthetic parameters (PTs) and 4 morphological traits (MTs) in

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a rice population, which consists of 204 USDA-curated minicore accessions collected globally and 11 elite Chinese rice cultivars in both Beijing (BJ) and Shanghai (SH). To identify key components responsible for variance of biomass accumulation, we applied a stepwise feature selection approach based on linear regression models. Though there are large variations in photosynthetic parameters measured in different environments, we observed that photosynthetic rate under low light ($A_{low}$) was highly related to biomass accumulation and also exhibited high genomic inheritability in both environments, suggesting its great potential to be used as a target for the future rice breeding programs. Large variations in $A_{low}$ among modern rice cultivars further suggest great potential of using this parameter in contemporary rice breeding for improvement of biomass and hence yield potential.

**Keywords:** SNP-based heritability, biomass, photosynthetic traits under low light, linear regression model.

**Abbreviations:** $A$: photosynthetic rates under high light; $A_{low}$: photosynthetic rates under low light; Biomass: above-ground biomass; $C_i$: internal CO$_2$ under high light; $C_{i,low}$: internal CO$_2$ under low light; $F_v/F_m$: maximum PSII efficiency; $g_s$: stomatal conductance under high light; $g_{s,low}$: stomatal conductance under low light; GEs: growth environments; $h^2_{SNP}$: SNP-based heritability; $L_s$: stomatal limitation under high light; MTs: morphological traits; PTs: Photosynthetic traits; LfThck: leaf thickness; $L_{s,low}$: stomatal limitation under low light; PltHt: plant height; SPAD: SPAD values; Tiller: Tiller number; WUE: water use efficiency under high light; $W_{low}$: water use efficiency under low light.
Introduction

Improving photosynthetic efficiency is regarded as a major target to improve crop biomass production and yield potential (reviewed by Zhu et al., 2010; Long et al., 2006). The canopy photosynthetic efficiency, which is determined by leaf area index, canopy architecture, and leaf photosynthetic properties, plays an important role in determining the biomass accumulation (Long et al., 2006; Zhu et al., 2012).

Historically, improvement of canopy architecture, i.e. creating cultivars with semi-dwarf architecture, more erect leaves, and higher leaf area index, has played an important role in traditional crop breeding (Hedden 2003; Peng et al., 2008), in contrast, the improvement of leaf photosynthetic properties has played a minor or no role during this process. Broadly, there are two major approaches to improve photosynthetic efficiency, i.e. by genetically engineering photosynthetic efficiency if an engineering target is well defined and by conventional crop breeding, i.e. identifying those lines with superior photosynthetic efficiency and then crossing this superior photosynthetic property into desired target cultivars (Long et al., 2006; Gepts, 2002). In either case, the major challenge now is to define effective photosynthetic traits which can lead to enhanced biomass production. We have earlier demonstrated that a system approach can be used to identify new targets to improve photosynthesis by combining systems modeling and an evolutionary algorithm (Zhu et al., 2008). The identified targets to improve photosynthesis have been transgenically tested both inside the lab and also in the field (Rosenthal et al., 2011; Simkin et al., 2015). Similarly, increase the speed of recovery from photoprotection has been demonstrated to be a major approach to increase canopy photosynthesis and crop yield potential (Zhu et al., 2004), which has been recently validated in model crop species tobacco in the field (Kromdijk et al., 2016). This success of enhancing biomass production through manipulation of photosynthesis clearly demonstrates that there is huge potential to improve photosynthetic efficiency for greater biomass and yield production.
Besides using a systems approach, another potentially rewarding approach to identify parameters related to biomass production is through mining natural variations (Flood et al., 2011; Lawson et al., 2012). The systems approach, to certain degree, increases the potential range of physiological parameters that can be explored than observed in existing cultivars. However, the success of this approach relies on availability of highly sophisticated and accurate systems models for the process under study. The advantage of mining natural variation is that we can collect biomass data and many physiological parameters for a large number of germplasms simultaneously, which facilitates the identification of parameters before availability of highly mechanistic models for the involved processes.

So far, however, large scale systematic studies of natural variations of photosynthetic parameters in major crops are scarce. Driever et al., (2014) reported natural variations of photosynthetic parameters in 64 elite wheat cultivars and found that though there are significant variation in photosynthetic capacity, biomass and yield, no correlation exists between grain yield and photosynthetic capacity. They suggested that during the breeding process, some traits might have been unintentionally selected out and hence photosynthetic efficiency should be a major target to utilize during the future wheat breeding (Driever et al., 2014; Carmo-Silva et al., 2017). Similar experiments have been conducted in rice which reached similar conclusions, i.e. leaf photosynthetic rate measured under saturating light levels do not show positive correlation with biomass accumulation (Jahn et al., 2011). On the first sight, this is rather contradictory to current theory of photosynthesis. However, if we consider the canopy that the overall crop light use efficiency, where biomass accumulation can be used as a surrogate, is determined by the total canopy photosynthesis, instead of leaf photosynthesis. Indeed, our earlier modeling work showed that light-limited photosynthesis can contribute up to 70% of the total canopy photosynthetic CO₂ uptake rates, even at a moderate leaf area index of 4.8 (Song et al., 2013). The proportion of light-limited photosynthesis will be even high under either high leaf area index or under future elevated CO₂ conditions (Zhu et al., 2012; Song et al., 2013). Large scale surveys of rice grain yield, harvest index and biomass accumulation for rice cultivars released since 1966 have shown clearly that the grain yield of cultivars released after 1980 were highly correlated to biomass accumulation, suggesting improved canopy photosynthesis during the recent rice breeding (Peng et
In this study, we aim to identify leaf photosynthetic parameters that are highly correlated with biomass accumulation, a surrogate of canopy photosynthesis. To do this, we surveyed a large number of leaf photosynthetic parameters and crop architectural parameters at two different locations in China, i.e. Shanghai and Beijing. In this study, to enable comprehensive survey of parameters relevant to canopy photosynthesis, we measured photosynthetic parameters not only under high light but also under limiting light conditions, with the intention to examine whether photosynthetic rates under low light are positively correlated with biomass accumulation. Finally, to minimize the potential complexity of source sink interaction during the grain filling stage, we used biomass accumulation before flowering to avoid the complexity of source sink interaction (Chang et al., 2017). To maximize the genetic diversity utilized in this study, we used both a 215 global rice diversity population consisting of 204 minicore accessions and 11 elite Chinese rice cultivars. Our result revealed that photosynthetic rate under low light ($A_{\text{low}}$) is highly correlated with biomass accumulation in this diverse rice germplasm population under both Beijing and Shanghai environments. Genetic analysis further shows that $A_{\text{low}}$ is under strong genetic control and hence are amenable for breeding or genetic manipulations. The large variations of $A_{\text{low}}$ in modern rice variations and high genetic inheritance suggest that $A_{\text{low}}$ can be used as a promising target in rice marker assisted breeding.

Results

Variability of the parameters in the global rice diversity panel

As shown from Table 1, natural variations for both 14 photosynthetic traits (PTs) and 4 morphological traits (MTs) in Beijing (BJ) and Shanghai (SH) conditions showed different levels of heterogeneity. The percentage genetic variation (PGV) is used to represent the levels of natural variation of traits. The PGV is calculated by the differences between extreme values over mean value in the population (see M&M for more details). The values of PGV in BJ ranged from 3.6 to 197.6 for PTs, and ranged
from 77.2 to 227.9 for MTs; while the values of PGV in SH ranged from 21.5 to 280.1
for PTs and ranged from 85.9 to 170.0 for MTs. The trait with minimum natural
variation is $F_v/F_m$ and its PGV under BJ/SH environmental conditions is only 12%. For
gas exchange related parameters under full light, the PGV values across the two
conditions decreased as follows: stomatal conductance under normal light ($g_s$) >
stomatal limitation (Ls) > water use efficiency (WUE) > photosynthetic CO$_2$ uptake
rate ($A$) > internal CO$_2$ concentration under normal light ($C_i$), while the PGV values of
these parameters under low light decreased as follows: water use efficiency under low
light ($W_{low}$) > stomatal limitation under low light ($L_{s_low}$) > photosynthetic CO$_2$ uptake
rate under low light ($A_{low}$) > stomatal conductance under low light ($g_{s_low}$) > internal CO$_2$
concentration under low light ($C_{ilow}$) (Table 1). The PGV of both dark respiration ($A_{dark}$)
and stomatal conductance under dark ($g_{sdark}$) were at least 120%, which was two times
higher than the PGV of the SPAD value. For morphological traits (Table 1), PGV
values showed drastic differences between experiments in BJ/SH environmental
conditions. The ranking of PGVs for biomass, tiller number, and leaf thickness
gradually decreased under BJ/SH environmental conditions. Most of the MTs showed
higher variations in PGV values under the BJ environment than those under SH, except
for the PGV of plant height (Table 1).

Estimation of SNP-based heritability ($h^2_{SNP}$) on a functional trait provides the
information about whether this particular trait is under strong genetic control and hence
can be used as a potential parameter during crop breeding. SNP-based heritabilities
($h^2_{SNP}$) of PTs were in range of < 0.001 to 0.72 in BJ/SH environmental conditions
(Table 1). Among these PTs, only 4 PTs exhibited significant $h^2_{SNP}$ under BJ/SH
environmental conditions, including WUE, $A_{low}$, $A_{dark}$, and SPAD (Table 1). For the MTs,
biomass accumulation and tiller number showed high $h^2_{SNP}$ under BJ/SH
environmental conditions (Table 1).

We further employed two-way ANOVA to analyze genotype × environment interaction
with regards to PTs and MTs. Results show that all PTs and MTs were significantly
different between BJ and SH environments. On one hand, we found strong
environmental effects on most of the collected PTs and MTs (Table 2); in contrast, 12
out of 18 collected traits were significantly affected by genotype factor, except $L_s$, $g_{s_low}$,
$C_{ilow}$, $L_{s_low}$, $g_{sdark}$ and leaf thickness (Table 2). Only $C_{ilow}$ was not significantly affected
by environment and genotype interactions (Table 2).

**Correlation between biomass and other biological parameters**

Pearson correlation coefficient was determined to evaluate the relatedness of biomass with different PTs and MTs under BJ/SH environmental conditions (Fig. 1; Table S1; Fig. S2; Fig. S3). As shown in Fig. 1 and Table S1, strong correlations were observed between PTs under both normal light and low light conditions when datasets measured under BJ/SH environmental conditions were combined. Fig. 2 shows the correlation between MTs and PTs in BJ/SH environmental conditions (Fig. 2; Table S2). Results reveal that $A$, $g_s$, $C_i$, $A_{\text{low}}$, $W_{\text{low}}$, $C_{\text{llow}}$, $F_v/F_m$, and SPAD exerted positive correlation with plant height, tiller number and biomass. On the other hand, WUE, $L_s$, $L_{s\text{low}}$, and $A_{\text{dark}}$ exerted negative correlation with plant height, tiller number, leaf thickness, and biomass. As expected, there is huge variation in the measured PTs between BJ and SH environmental conditions, suggesting the strong environment impacts on most of the PTs (Fig 3), as shown earlier by the strong environment effect on these parameters (Table 2). Certain photosynthetic parameters, including $A$, $g_s$, $A_{\text{low}}$ and SPAD, showed high correlation index ($R^2$) between both BJ and SH sites (Fig. 3).

**Linear regression model and stepwise feature selection**

To identify the key parameters that dominate biomass variation under BJ/SH environmental conditions, we employed a linear regression model (LRM) with a stepwise optimization method based on the Akaike information criterion (AIC). We first evaluated the prediction accuracy of the derived LRMs under BJ, SH and combined datasets (Fig. 4). Our approach used a training dataset consisting of 90% of the original data and a test dataset of the remaining 10% of the data (see Materials and Methods for details). As shown in Fig. 4, the models predicted the values of biomass under BJ, SH and combined environments ($P < 0.001$) with $R^2$ between the predicted and measured biomass ranging from 0.32 to 0.76 in training dataset (Fig. 4, A, C and E). Furthermore, the model predicted the test dataset with $R^2$ ranging from 0.37 to 0.72 across the three models (Fig. 4, B, D and F). These results suggest that the derived LRMs can predict the biomass accumulation with a high level of confidence.

The PTs identified in these three LRMs were used for further analysis. The PTs
identified to highly correlated with biomass accumulation from different datasets were shown in Fig. 5 and Table S3. The fitting equations under BJ/SH environmental conditions were listed as followings: The obtained equations under BJ/SH environmental conditions are: Biomass(BJ) = 0.096 gs + 0.115 A low + 0.311 × Plant height + 0.355 × Tiller number; Biomass(SH) = 0.053 L s - 0.081 WUE + 0.152 A low + 0.077 L slow + 0.127 × Leaf thickness + 0.341 × Plant height + 0.671 × Tiller number; Biomass (Combine) = 0.072 gs + 0.169 Ci - 0.089 L s + 0.107 A low + 0.192 W low - 0.145 L slow + 0.139 SPAD + 0.448 × Plant height + 0.556 × Tiller number. Two PTs (gs and A low) were identified in models for BJ; 4 PTs (WUE, L s, L slow and A low) were identified for SH and 7 PTs (gs, W low, SPAD, Ci, L s, L slow, and A low) were identified for the combined environments. These large variations in the identified PTs responsible for biomass accumulation in different locations reflect the strong environment impacts on many photosynthetic parameters. Surprisingly, even under such great impacts of environments on photosynthetic parameters, A low was consistently identified to be closely associated with biomass accumulation in BJ/SH environmental conditions (Fig. 5). gs was also shown to be a major variable associated with biomass accumulation in both the BJ and the combined datasets. The L s and L slow were identified in both SH and combined datasets (Fig. 5). Based on these obtained LRM s, the PTs expected to be increased to improve biomass accumulation are gs, A low, W low and SPAD, while those need to be decreased are WUE, L s, and L slow (Table S3).

**Ranking of Elite Cultivars within minicore Collection**

To further evaluate the scope to manipulate A low for improved biomass production, we examined the distribution of A low among the minicore panel and the distribution of A low in 11 current elite rice lines (Fig. 6). Under the BJ environment, A low exhibits a normal distribution in the minicore population (Fig. 6A) and also there is a huge variation of A low among the 11 elite rice lines (Fig. 6B). The distribution pattern and ranking of A low in SH environment are shown in Fig S1. We further evaluated the potential improvements of A low by calculating the percentage difference (PD) between A low of the elite lines and the highest A low observed in the minicore population. There are potentially 76.77% and 85.49% improvement in DHX-Z and ZH11 respectively if their corresponding A low can reach the maximal A low in minicore, i.e. that for P4140.

**Discussion**
Natural variation in photosynthetic traits (PTs) is a largely unexploited resource which can be used to identify new targets to breed or engineer higher photosynthetic efficiency (Flood et al., 2011; Driever et al., 2014). Comparing the relatively long-term perspective of engineering photosynthesis for greater yield (Long et al., 2015), mining natural variations of photosynthesis using natural population can lead to reasonably short-term (<5 years) crop improvements (Parry et al., 2011). In this study, we explored natural variations in photosynthetic parameters in rice that might are related to biomass accumulation, a surrogate of canopy photosynthesis. Using linear regression models (LRMs) constructed under different environments, we identified photosynthetic rates under low light ($A_{\text{low}}$) as a major photosynthetic parameter with high correlation with biomass accumulation under two drastically different environments. Here we briefly discuss the major findings of this study and their implications for rice breeding.

**Natural variations and heritability of all photosynthetic parameters**

Since 1960s, researchers started working on improving photosynthesis through introgression, e.g. in soybean (Ojima, 1974). However, the progress was rather limited because on one hand it remained unclear what photosynthetic traits (PTs) should be the targets, and on the other hand, there were no effective molecular marks related to PTs defined well enough to be used in breeding programs (Flood et al., 2011). The aim of this study is to identify highly heritable PTs relevant to biomass production under different environments. Since screening PTs is labor-intensive and time-consuming, instead of using the global rice core collection of 1794 accessions, we used a minicore diversity panel consisting of 204 global rice accessions, which is sufficiently diverse to effectively represent the original core collection (Agrama et al., 2009) and also is manageable especially for detailed photosynthesis phenotyping.

As expected, our data suggest that there are substantial variations among photosynthetic parameters under BJ/SH environmental conditions (Table 1), suggesting there is genetic diversity in PTs in rice that can be potentially exploited. Furthermore, our heritability analysis shows that $h^2_{\text{SNP}}$ in many PTs, including SPAD, stomatal limitation ($L_s$) and WUE under BJ/SH environmental conditions, were around 0.6~0.7, which are closed to some earlier reports (Schuster et al., 1992;
McKown et al., 2014; Geber and Dawson, 1997; Table 1), suggesting that these parameters are under strong genetic control in different species. It is worth emphasizing that, in this study, our estimate of heritability $h^2_{SNP}$ utilizes not only casual genes as in the traditional variance method (reviewed by Zaitlen and Kraft, 2012), but also considers other single nucleotide polymorphism markers ($h^2_{SNP}$) (Yang et al., 2011). The observed high levels of heterogeneity and relatively high $h^2_{SNP}$ for many PTs suggest that these traits can be used as potential candidates in marker assisted breeding for rice (Ackerly et al., 2000).

A low is a photosynthetic trait which is highly correlated with biomass accumulation under different environments

In this study, a stepwise feature selection approach was applied to the data collected under either BJ or SH environments. With this method, we identified two PTs, i.e., gs and A low, in both the BJ and its combined datasets (Fig. 5). Both gs and A low exhibited high correlation with biomass (Fig. 2; Fig. S2; Fig. S3). The values of both parameters show strong correlation between BJ and SH environments (Fig. 3). gs showed a high $h^2_{SNP}$ and substantial natural variation among rice cultivars under BJ/SH environmental conditions (Table 1, 2), suggesting that gs is a good parameter to be used in rice breeding. In fact, gs screening based on thermal imaging (Takai et al., 2010b) has already been used in some breeding programs, e.g. the wheat yield potential breeding in the physiology breeding program of CYMMIT (Rajaram et al., 1994). It is worth noting that, in addition to gs itself being potentially important parameter for breeding, faster response of gs to fluctuating light can be an adaptive trait for rice under severe drought conditions (Qu et al., 2016).

Remarkably, the A low instead of A under normal light was identified to be a photosynthetic parameter highly correlated with biomass accumulation under BJ, SH and combined datasets (Fig. 5; Table S3). A low is also under strong genetic control, as shown by its high $h^2_{SNP}$ (Table 1). Therefore A low is a promising target for future rice breeding improvements. This finding is remarkable since although it has been long recognized that canopy-, instead of leaf-, photosynthesis is a major determinant of biomass accumulation, so far, direct experimental evidence supporting the importance of photosynthetic efficiency under low light is lacking. The strong correlation between
A$_{\text{low}}$ and biomass accumulation reported here strongly support the notation that photosynthetic CO$_2$ uptake of the lower layer leaves, which usually experiences low light levels, contribute substantially to the overall canopy photosynthesis and hence biomass production. This finding increases the repertoire of parameters known so far that can potentially improve canopy photosynthesis, which includes faster speed of recovery from photoprotective status (Zhu et al., 2004), rapid recovery of stomata conductance under fluctuating light (Lawson and Blatt, 2014; Qu et al., 2016), and Rubisco with optimized kinetic properties (Zhu et al., 2004). Large scale genetic screening of these different parameters and gene identification in this global minicore are underway in our laboratory.

Potential value of the identified traits in current rice breeding

Natural distribution of A$_{\text{low}}$ across the minicore panel yielded a normal distribution (Fig. 6 B); furthermore, there are substantial variation of A$_{\text{low}}$ in the modern elite rice cultivars (Table 3; Fig. 6), suggesting large space to improve A$_{\text{low}}$ to enhanced biomass production in contemporary elite rice cultivars. By comparing the value of A$_{\text{low}}$ in the modern elite cultivars with the extreme values observed in the minicore diversity panel under the BJ environment, we identified candidate donors that can be used as genetic resources for A$_{\text{low}}$. For example, 76.77% and 85.49% improvement of A$_{\text{low}}$ can be achieved in DHX-Z and ZH11 (elite cultivar), respectively (Table 4), if the causal genes (or QTLs) controlling A$_{\text{low}}$ in P4140 can be transferred into these two cultivars.

Conclusion

By mining natural variations of photosynthesis related traits in a natural rice diversity panel, here we found that, among many photosynthetic parameters, photosynthetic rates under low light (A$_{\text{low}}$) is highly correlated with biomass accumulation under different environments. Furthermore, A$_{\text{low}}$ shows high level of variability among contemporary elite rice lines and it has a high inheritability. All these suggest that A$_{\text{low}}$ is a promising target for the future rice breeding programs.

Materials and Methods
Plant material

The accessions from the USDA collected minicore rice diversity panel are from 76 countries covering 15 geographic regions, which consists of six groups, *indica* (35.4%), *aus* (18.7%), *tropical japonica* (18.2%), *temperate japonica* (15.2%), *aromatic* (3.0%) and their admixtures (9.6%) (Agrama et al., 2010; Li et al., 2010). The population accounts for 12.1% of the global rice core accessions and displayed 100% coverage in genetic variation (Agrama et al., 2010). In current study, we used 204 out of 217 accessions in the minicore population since the remaining 13 accessions have extremely long growing seasons. In addition, we used 11 Chinese elite rice cultivars (WCC1, WCC2, DHX-Z, HE19, KY131, XS134, ZH11, MH63, KALS, 9311, WY-4) (Hamdani et al., 2015).

Measurements of leaf gas exchange

The 204 minicore panel and 11 elite rice lines were transplanted under two environments, i.e. Beijing (BJ) (116.3943°E, 39.9820°N) in May 2013 and Shanghai (SH) (121.4530°E, 31.0428°N) in May 2015. Averaged atmosphere temperature under BJ/SH environmental conditions, during the growth periods from transplanting to booting stage until large-scale measurements started, which spanned around 60 days, were around 24.8 ± 3.1 and 25.5 ± 4.4 °C, respectively. Experiments were conducted in pots and detailed experimental procedures were described in Hamdani et al., (2015). Briefly, plants were sowed in 12L pots filled with commercial peat soil (Pindstrup Substrate no. 4, Pindstrup Horticulture Ltd, Shanghai, China). For each accession, six plants were planted in two pots with three plants per pot. Two pots for the same accession were arranged close together to ensure formation of canopy. Pots from different accessions were separated to avoid shading from a different accession. During the growth period, plants were exposed to natural sunlight and were irrigated daily. Fertilizers were applied twice per month. Experiments of leaf gas exchange were conducted at 60 days after emergence (DAE). For each accession, we used four replicates during the measurements of gas exchange related parameters. All the photosynthesis measurements were finished within 10 days. To minimize the potential errors introduced by potential growth stage differences, we measured photosynthetic parameters from accession 1 through 215 sequentially for the first and third replicates, and then from accession 215 to 1 sequentially for the second and fourth replicates.
Plants were acclimated in a controlled room with a temperature around 27 °C and the PPFD around 600 µmol m⁻² s⁻¹ for at least 60 minutes before gas exchange measurements. During the measurements, two levels of photosynthetic photon flux density, i.e. 1200 µmol mol⁻¹ s⁻¹ (normal light) and 100 µmol mol⁻¹ s⁻¹ (low light), were used. Four portable infrared gas exchange system (Li-6400XT, Li-COR Inc., Lincoln, NE, USA) were used simultaneously. An automatic program was applied to measure gas exchange traits under two light levels, traits under normal light include photosynthetic rates (A), stomatal conductance (gₛ), internal CO₂ (Cᵢ), water use efficiency (WUE) and stomatal limitation (Lₛ); traits under low light include Aᵢ, Gₛᵢ, Cᵢᵢ, Wᵢ and Lₛᵢ (see abbreviation section for more details). The process of such program is as following: leaf was first maintained under a PPFD of 1200 µmol m⁻² s⁻¹ for at least 5 minutes or until gₛ reached a steady state, then PPFD was changed to 100 µmol m⁻² s⁻¹ for 25 minutes allowing gₛ to approach steady state as described from Qu et al., (2016). During the measurements, the leaf temperature was maintained at 25 °C and relative humidity was maintained at ~ 75%, the reference CO₂ concentration was set as 400 µmol mol⁻¹ and we used the top fully expanded leaves for this measurements. Data were automatically recorded and the average values within the last 1 minute before light switch were used for data analyzing.

**Measurements of dark respiration and maximal quantum yield**

Experiments for dark respiration were conducted at 60 DAE. Respiration rates were determined as net rates of CO₂ efflux in darkness during night after 8:00 pm according to Bunce (2007). Leaf temperatures were set to 25°C, reference CO₂ concentration was set to be 400 µmol mol⁻¹, and light level was set to be 0 µmol mol⁻¹ s⁻¹.

Multi-Function Plant Efficiency Analyzer (M-PEA) chlorophyll fluorometer (Hansatech, Kings Lynn, Norfolk, UK) was used to measure Fᵥ/Fᵢ, the maximal quantum yield of photosystem II, following Hamdani et al., (2015). Fᵢ represents the maximum chlorophyll fluorescence, Fₒ is the minimum chlorophyll fluorescence and Fᵥ = Fᵢ-Fₒ (Oxborough and Baker, 1997; Huang et al., 2016; Essemine et al., 2017).

**Measurements of SPAD and leaf thickness**

Experiments for SPAD and leaf thickness were conducted at 60 DAE. To estimate leaf
total chlorophyll content and leaf thickness, SPAD 502 Plus Chlorophyll meter (Spectrum Technologies, Inc.) (Takai et al., 2010a) and Micrometer screw (Mitutoyo Co.) were used, respectively. For each leaf, the chlorophyll content was estimated as the mean of 5 chlorophyll content measurements at different positions in the middle section of the leaf. Four replicates from four different plants were determined for both leaf chlorophyll concentration and leaf thickness.

**Measurements of plant morphological traits**

The above-ground biomass accumulation (biomass), plant height (PhtHt), and tiller number (Tiller) were determined at 60 DAE according to Qu et al., (2016). At least four replicates were measured for each parameter above. Samples for biomass determinations were kept at 120 °C for 1 hour and then under 70 °C for at least 24 hours in a baking oven until constant weight is reached before weights of biomass or leaf segments were measured.

**Regression model between biomass and morphological and photosynthetic traits**

We used a linear regression model (LRM) to capture correlation of biomass with PTs and MTs. The model is defined as follows:

\[
y = \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_v x_v + \epsilon
\]

Where \(y\) is a vector representing biomass values of each rice accession, \(x\) is a vector of independent variables, \(\beta\) is weighted coefficients corresponding to \(x\), and \(\epsilon\) is an error vector. The model was constructed with a stepwise manner, which can identify highly relevant parameters and remove low relevant parameters based on the Akaike information criterion (AIC) according to Jin et al., (2014). In practice, a training dataset including 90% items of the whole dataset was randomly extracted from the original dataset and the remaining 10% data were used as a test dataset (Kawamura et al., 2010; Iwasaki et al., 2013). The training dataset was first defined to build the regression model, and then an independent validation was conducted on the test dataset to check performance of the model.

**Estimation of SNP-based heritability**

The GCTA software (Version 1.25.2) (Yang et al., 2011) was employed to estimate SNP-based heritability \(h^2_{SNP}\) of 23 functional traits using 2.3M filtered SNPs of the minicore population(Wang et al., 2016). GCTA implements the method in two steps,
i.e., generating a high-dimensional genetic relatedness matrix (GRM) between individuals and then estimating the variance explained by all SNPs by a restricted maximum likelihood (REML) analysis of the phenotypes with GRM (Yang et al., 2011). The significance of $h^2_{\text{SNP}}$ is assessed by likelihood ratio test (LRT), which is the ratio of likelihood under the alternative hypothesis ($H_1$: $h^2_{\text{SNP}} \neq 0$) to that under the null ($H_0$: $h^2_{\text{SNP}}=0$). The LRT and its corresponding $p$ value were reported in the GCTA output file.

**Data analysis**
In order to quantitatively evaluate the genetic variation of biological traits in the combined population, percentage genetic variation (PGV) was calculated as $\left(\frac{X_{\text{max}}-X_{\text{min}}}{\bar{X}}\times 100\right)\%$, where $X_{\text{max}}$, $X_{\text{min}}$ and $\bar{X}$ stands for maximum, minimum and mean value in the population, respectively (Gu et al., 2014). The Pearson correlation coefficient was calculated using R package (Corrplot) (3.2.1 version).

**Supplemental data:**

**Supplemental Table S1.** Correlation of photosynthetic traits and morphological traits in global minicore panel and elite rice cultivars across the experiments of Beijing (BJ) and Shanghai (SH) sites.

**Supplemental Table S2.** Correlation of photosynthetic traits with morphological traits under Beijing (BJ) and Shanghai (SH) experiments.

**Supplemental Table S3.** Feature selection across Beijing, Shanghai and combined sites.

**Supplemental Figure S1.** Trait distribution of elite cultivars and the minicore accessions under the SH environment.

**Supplemental Figure S2.** Correlation of photosynthetic traits with biomass under the Beijing (BJ) environment.

**Supplemental Figure S3.** Correlation of photosynthetic traits with biomass under the Shanghai (SH) environment.
Supplemental Table S1. Correlation of photosynthetic traits and morphological traits in global minicore panel and elite rice cultivars across the experiments of Beijing (BJ) and Shanghai (SH) sites. For trait abbreviations refer to Table 1. The colors in cells ranging from red to green represent the correlation coefficient from negative to positive correlation.

Supplemental Table S2. Correlation of photosynthetic traits with morphological traits under Beijing (BJ) and Shanghai (SH) experiments. The values represent Pearson correlation coefficient under BJ/SH experiments. Asterisks “*”, “**” were depicted as P-value<0.05, 0.01, respectively. Refer to Table 1 for detailed abbreviation of each trait.

Supplemental Table S3. Feature selection across Beijing, Shanghai and combined sites. Traits abbreviations were as mentioned in detail in title of Table 1. SD and P signify standard deviation and P-value, respectively.

Supplemental Figure S1. Trait distribution of elite cultivars and the minicore accessions under the SH environment. A: distribution of photosynthetic rates under low light ($A_{\text{low}}$) of elite cultivars within the minicore accessions. B: Histogram representing the distribution of $A_{\text{low}}$ in the minicore diversity panel. The enclosed numbers represent: WCC1①, WCC2②, DHX-Z③, HE19④, KY131⑤, XS134⑥, ZH11⑦, MH63⑧, KALS⑨, 9311⑩, and WY-4⑪.

Supplemental Figure S2. Correlation of photosynthetic traits with biomass under the Beijing (BJ) environment. The values of photosynthetic traits and biomass were normalized ranging from 0 to 1. The values of Pearson correlation coefficient (R) were calculated. Asterisks “*”, “**” represent P value < 0.05, and 0.01, respectively. The abbreviated PT at right-bottom corner of each panel is as described in details in Figure 1.

Supplemental Figure S3. Correlation of photosynthetic traits with biomass under the Shanghai (SH) environment. The values of photosynthetic traits and biomass were normalized ranging from 0 to 1. The values of Pearson correlation coefficient (R) were calculated. Asterisks “*”, “**” represent P value < 0.05, and 0.01, respectively. The abbreviated PT at right-bottom corner of each panel is as described in details in Figure 1.
Acknowledgments

This work thanks the anonymous reviewers for constructive comments which helped us improve our revision. This work was supported by CAS Strategic Research Project [grant number XDA08020301], Shanghai Municipal Natural Science Foundation [grant number 17YF1421800] and [grant number 14ZR1446700] and Bill & Melinda Gates Foundation [grant number OPP1014417].

Figure Legends

Figure 1. Correlation of photosynthetic traits (PTs) and morphological traits (MTs) in the global minicore panel and elite rice lines. Data were combined from Beijing (BJ) and Shanghai (SH) experiments. The abbreviations of PTs are: A: photosynthetic rates under high light; A\text{low}: photosynthetic rate under low light; Biomass: above-ground biomass; C\text{i}: internal CO\textsubscript{2} under high light; C\text{ilow}: internal CO\textsubscript{2} under low light; F\textsubscript{v}/F\textsubscript{m}: maximum PSII efficiency; g\text{S}: stomatal conductance under high light; g\text{s}\text{low}: stomatal conductance under low light; L\text{s}: stomatal limitation under high light; L\text{s}\text{low}: stomatal limitation under low light; SPAD: SPAD values; WUE: water use efficiency under high light; W\text{low}: water use efficiency under low light; PltHt: plant height; Tiller: tiller number; Thick: leaf thickness; Biomass: biomass accumulation.

Figure 2. Graphic representation of correlations of different PTs with MTs in the global minicore panel and elite rice lines under Beijing (BJ) and Shanghai (SH) environments. Shaded area at the center represents negative correlation. Trait abbreviations are given in Table 1.

Figure 3. Self-correlation of each photosynthetic trait in the global minicore panel and elite rice lines grown in Beijing (BJ) and Shanghai (SH) environments. The values of Pearson correlation coefficient (R) were calculated. Asterisks “*”, “**” represent $P$ value < 0.05, and 0.01, respectively. The abbreviated PT at right-bottom corner of each panel is as reported in details in Figure 1.

Figure 4. Model construction and cross-validation in the global minicore panel and elite rice lines under Beijing (A and B), Shanghai (C and D) and the combined (E and F) datasets. The training dataset consists of 90% of the whole dataset and the remaining 10% items were used as a test dataset (see Material and Method for details). Predicted values of biomass versus observed values of biomass were used...
during the cross-validation. Determination index ($R^2$) reflects the accuracy of regression between predicted and observed values.

**Figure 5.** Features selections analysis on photosynthetic traits (PTs) using Linear Regression Models (LRMs). Key PTs identified by models were represented constructed under Beijing (BJ), Shanghai (SH) and their combined environments (Combine). The equations under BJ, SH and Combined environments are listed as followings: Biomass(BJ) = 0.096 $g_s + 0.115 A_{low} + 0.311 \times \text{Plant height} + 0.355 \times 0.127 \times \text{Leaf thickness}$ $+ 0.341 \times \text{Plant height} + 0.671 \times \text{Tiller number}; \text{Biomass (SH)} = 0.053 L_s - 0.081 \text{WUE} + 0.152 A_{low} + 0.077 L_{slow} + 0.127 \times \text{Leaf thickness} + 0.341 \times \text{Plant height} + 0.671 \times \text{Tiller number}; \text{Biomass (Combine)} = 0.072 g_s + 0.169 C_i - 0.089 L_s + 0.107 A_{low} + 0.192 W_{low} - 0.145 L_{slow} + 0.139 \text{SPAD} + 0.448 \times \text{Plant height} + 0.556 \times \text{Tiller number.}

**Figure 6.** Trait distribution of elite cultivars and the minicore accessions under the Beijing (BJ) environment. A: Histogram representing the distribution of photosynthetic rates under low light ($A_{low}$) in the minicore diversity panel. B: Phenotypic distribution of $A_{low}$ of elite cultivars within the minicore accessions. The enclosed numbers represent: WCC1①, WCC2②, DHX-Z③, HE19④, KY131⑤, XS134⑥, ZH11⑦, MH63⑧, KALS⑨, 9311⑩, and WY-4⑪.
Table 1. Natural variation and SNP-based heritability of PTs in the global minicore panel and elite rice lines grown in Beijing (BJ) and Shanghai (SH) environments. PGV was calculated as described in Materials and Methods. Symbols "*, **, ***" represent P< 0.05, 0.01 and 0.001, respectively. The abbreviations of PTs are: A: photosynthetic rates under high light; A\textsubscript{low}: photosynthetic rates under low light; Biomass: above-ground biomass; C\textsubscript{i}: internal CO\textsubscript{2} under high light; C\textsubscript{i}\textsubscript{low}: internal CO\textsubscript{2} under low light; F\textsubscript{v}/F\textsubscript{m}: maximum PSII efficiency; g\textsubscript{s}: stomatal conductance under high light; g\textsubscript{s}\textsubscript{low}: stomatal conductance under low light; L\textsubscript{s}: stomatal limitation under high light; L\textsubscript{s}\textsubscript{low}: stomatal limitation under low light; SPAD: SPAD values; WUE: water use efficiency under high light; W\textsubscript{low}: water use efficiency under low light. h\textsuperscript{2}\textsubscript{SNP} represents SNP-based heritability. The two grey selected rows mean that the data is available only for BJ site. n: represents the accessions number.

<table>
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<tr>
<th>Traits</th>
<th>Sites</th>
<th>N</th>
<th>Range</th>
<th>Mean ± SD</th>
<th>PGV</th>
<th>h\textsuperscript{2}\textsubscript{SNP}±S E</th>
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</thead>
<tbody>
<tr>
<td>A (μmol m\textsuperscript{-2} s\textsuperscript{-1})</td>
<td>BJ</td>
<td>214</td>
<td>13.65~28.19</td>
<td>21.02±3.00</td>
<td>69.17</td>
<td>0.13±0.07</td>
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<tr>
<td></td>
<td>SH</td>
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<td>12.44~39.76</td>
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<td>0.15±0.03</td>
</tr>
<tr>
<td>g\textsubscript{s} (mmol m\textsuperscript{-2} s\textsuperscript{-1})</td>
<td>BJ</td>
<td>214</td>
<td>0.18~0.99</td>
<td>0.41±0.12</td>
<td>197.56</td>
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<tr>
<td></td>
<td>SH</td>
<td>186</td>
<td>0.14~1.16</td>
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<tr>
<td>WUE (mmol m\textsuperscript{-1})</td>
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<td>214</td>
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<td>C\textsubscript{i} (μmol mol\textsuperscript{-1})</td>
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<td>187</td>
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<td>L\textsubscript{s}</td>
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<td></td>
<td>SH</td>
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<td>0.15~0.51</td>
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<td>0.48±0.21**</td>
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<td>A\textsubscript{low} (μmol m\textsuperscript{-2} s\textsuperscript{-1})</td>
<td>SH</td>
<td>187</td>
<td>2.26~6.42</td>
<td>3.76±0.67</td>
<td>110.64</td>
<td>0.36±0.12*</td>
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<td>G\textsubscript{s}\textsubscript{low} (mmol m\textsuperscript{-2} s\textsuperscript{-1})</td>
<td>BJ</td>
<td>214</td>
<td>0.17~0.26</td>
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<td>200.00</td>
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<td>C\textsubscript{i}\textsubscript{low} (μmol mol\textsuperscript{-1})</td>
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<td>183</td>
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<td>-0.53±0.22</td>
<td>233.96</td>
<td>0.26±0.06*</td>
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### Table 2. Analysis of variance (F-values and significance) on effects of environments, genotype and environment × genotype interaction on each photosynthetic trait.

Stomatal conductance measured under low light (gs$_{low}$) and at night (gs$_{dark}$) were not determined under SH experimental condition. ND: no determination. Symbols "*, **, ***" were depicted as $P < 0.05$, 0.01 and 0.001, respectively. See Table 1 for the detailed abbreviations of the PTs.

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<th>Interactions</th>
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<td>A</td>
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<td>g$_s$</td>
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<td>WUE</td>
<td>6.795***</td>
<td>16.40***</td>
<td>10.360***</td>
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<td>C$_i$</td>
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<td>376.50***</td>
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<td>L$_s$</td>
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<td>135.80***</td>
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<td>A$_{low}$</td>
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<td>g$<em>{S</em>{low}}$</td>
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<td>ND</td>
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<td>W$_{low}$</td>
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<td>C$<em>{i</em>{low}}$</td>
<td>1.907</td>
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<td>L$<em>{s</em>{low}}$</td>
<td>0.397</td>
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<td>A$_{dark}$</td>
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<td>g$<em>{S</em>{dark}}$</td>
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<td>ND</td>
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<td>SPAD</td>
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<td>5.438***</td>
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<td>F$<em>{v}/$F$</em>{m}$</td>
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<td>Biomass</td>
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<td>PltHt</td>
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<td>Tiller number</td>
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<td>LfThck</td>
<td>0.463</td>
<td>986.00***</td>
<td>15.440***</td>
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Table 3. Comparison of photosynthetic rates under low light ($A_{\text{low}}$) between elite cultivars with those of the minicore accession showing highest $A_{\text{low}}$. Percentage difference (PD) was expressed as: $(A_{\text{low}}$ of extreme accession - $A_{\text{low}}$ of elite cultivar)/(A$_{\text{low}}$ of extreme accession) × 100%. P4140 is an accession in the minicore population which showed the highest values in $A_{\text{low}}$ in the BJ environment.

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<th>Elite accessions</th>
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<tr>
<td>WCC1</td>
<td>5.39±0.45</td>
<td>22.88</td>
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<td>WCC2</td>
<td>5.82±0.83</td>
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<td>DHX-Z</td>
<td>3.74±1.03</td>
<td>76.77</td>
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<td>HE19</td>
<td>5.93±0.29</td>
<td>11.68</td>
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<td>KY131</td>
<td>5.66±0.88</td>
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<td>XS134</td>
<td>4.87±0.51</td>
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<td>ZH11</td>
<td>3.57±0.60</td>
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<td>MH63</td>
<td>4.66±0.15</td>
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<td>KALS</td>
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<td>9311</td>
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Target accession  P4140
Reference

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variation in photosynthetic capacity, growth, and yield in 64 field-grown wheat

dehydrogenase-mediated cyclic electron flow to a shortage or lack in
ferredoxin-quinone oxidoreductase-dependent pathway in rice following

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Takai T, Yano M, Yamamoto T (2010b) Canopy temperature on clear and cloudy days can be used to estimate varietal differences in stomatal conductance in rice. F Crop Res 115: 165–170


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CrossRef: Author and Title
Google Scholar: Author Only Title Only Author and Title

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