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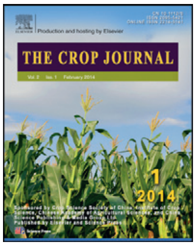

Three photosynthetic patterns characterized by cluster analysis of gas exchange data in two rice populations

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ABSTRACT

Plant photosynthetic rate is affected by stomatal status and internal CO_2 carboxylation. Understanding which process determines photosynthetic rate is essential for developing strategies for breeding crops with high photosynthetic efficiency. In this study, we identified different physiological patterns of photosynthetic rate in two different rice populations. Photosynthetic gas exchange parameters were measured during the flowering stage in two rice populations. Clustering and correlation analyses were performed on the resulting data. Five or six groups were defined by K-means clustering according to differences in net photosynthetic rates (P_n). According to differences in stomatal conductance (g_s) and carboxylation efficiency (CE), each group was clustered into three subgroups characterized by physiological patterns stomatal pattern, carboxylation pattern, and intermediate pattern. P_n was significantly correlated with g_s (r = 0.810) and CE (r = 0.531). P_n was also significantly correlated with g_s and CE in the three physiological patterns. The correlation coefficients were highest in the stomatal pattern (0.905 and 0.957) and lowest in the carboxylation pattern (0.825 and 0.859). Higher correlation coefficients between P_n and g_s or CE in the three physiological patterns indicate that clustering is very important for understanding factors limiting rice photosynthesis.

1. Introduction

Increasing leaf photosynthesis is an important way to increase biomass production and yield potential when the effects of other factors such as partitioning, nutrient responsiveness, and leaf area index have been minimized [1–3]. This realization has renewed interest in ways to improve photosynthesis at the individual leaf level. Besides engineering C_4 photosynthetic pathway into C_3 crops, another way is to use high-photosynthesis genetic resources of crops or their wild relatives.

Abbreviations: P_n, net photosynthetic rate; g_s, stomatal conductance; CE, carboxylation efficiency.

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Most attention at the leaf level has been focused on increasing the light-saturated photosynthetic rate (P_n), possibly because photosynthesis under light-limiting conditions is much more variable than under light saturation. Many studies on historical varieties of different crop species have revealed that P_n influences yield potential for crop improvement [4–8], suggesting that P_n is a useful parameter for improvement of photosynthesis by breeding.

Clear differences in P_n have been observed among rice varieties, species, and progeny derived from crosses between species [4,9–13]. However, the mechanism of variation in P_n is complex. Many studies have found that P_n is significantly correlated with stomatal conductance (g_s) [5,9,14], which describes the stomatal process affecting photosynthesis. P_n is also significantly correlated with Rubisco (Ribulose biphosphate carboxylase/oxygenase) content of the leaf [9,15] and carboxylation efficiency (CE) [16], which describes the biochemical processes affecting photosynthesis. Notably, the correlation between P_n and g_s is always higher than that between P_n and Rubisco content or CE. It is unclear which parameter, g_s or CE, would be more important in breeding crops with high photosynthetic rate.

In the present study we performed a multivariate statistical analysis of gas exchange parameter data obtained from two rice populations and found that different photosynthetic patterns are present in rice.

2. Materials and methods

2.1. Materials

Rice population A consisted of F_5 progenies derived from hybridization between the upland rice line $YF_{2\text{-}1}$ and sorghum variety Shennong 133. The cross was made by the pollen-tube pathway method [17] (performed by Zhao Fengwu, Dry Land Farming Institute, Hebei Academy of Agriculture and Forestry Sciences). At the F_1 generation, plants with different traits from the $YF_{2\text{-}1}$ were selected, followed by continuous pedigree selection from F_2 to F_5. For population B, the "new plant type" (NPT) rice line IR65598-110-2 was crossed with the wild rice *Oryza longistaminata* (IRRI accession number 101741). The progeny were backcrossed twice and the BC_2F_2 population was obtained at International Rice Research Institute (IRRI). The BC_2F_2 was screened in Beijing in an upland field for drought resistance and ecological adaptation. Six individuals that reached maturity were selected. Their segregating offspring were selected continuously and the BC_2F_5 populations were defined as population B. Owing to the two cycles of backcrossing, population B showed less variation than population A. The two populations were grown in a field using conventional management techniques. The most recently expanded leaves were selected for measurement at the heading stage.

2.2. Determination of gas exchange

The gas exchange parameters were determined on sunny, windless days from 9:30 to 11:30 a.m., using the LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA). Leaf temperature was controlled at 30 °C and photon flux density was controlled at 1400 μmol m^{-2} s^{-1}. Net photosynthetic rate (P_n), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), and transpiration rate (T_r) were recorded. Carboxylation efficiency (CE) was calculated as P_n/C_i [18,19].

2.3. Statistical analysis

All multivariate analyses and significance tests were conducted using SPSS 17.0 (SPSS Inc., Chicago, IL, USA). The K-means clustering method was used for cluster analysis. It differs from hierarchical clustering in several ways. First, the number of clusters is determined by rerunning the analysis for different numbers of clusters. Then, with the assigned cluster number, the maximum iterations are set at 50, the analysis is begun with an initial set of means, and cases are classified based on their distances from the centers. The algorithm repeatedly reassigns cases to clusters until cluster means do not change much between successive steps. Finally, the algorithm calculates the means of the clusters once again and assigns the cases to their final clusters.

3. Results

3.1. Classification of photosynthetic rate in the rice populations

The gas exchange parameters of 219 rice plants from population A and 204 plants from population B were determined. The P_n ranged from 13.6 to 30.9 μmol CO_2 m^{-2} s^{-1} and 16.1 to 33.2 μmol CO_2 m^{-2} s^{-1}. The histogram of P_n and the Q–Q plot (relating the

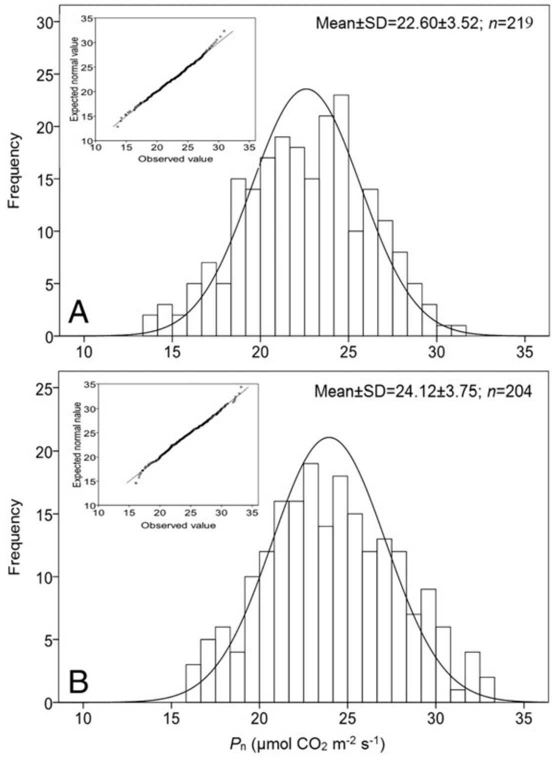

Fig. 1 – Normal distribution of net photosynthetic rate in rice populations A and B. The main plot shows the histogram and the inset shows the Q–Q plot of P_n. In population A, the P_n values of the two parents are 25.5 ($YF_{2\text{-}1}$) and 41.4 (Shennong 133) μmol CO_2 m^{-2} s^{-1}; in population A, the P_n values of the two parents are 24.5 and 34.3 μmol CO_2 m^{-2} s^{-1}.

Table 1 – Descriptive statistics of net photosynthetic rates in different groups.

	Population A				Population B			
	n	Range	Mean ± SE	CV (%)	*n*	Range	Mean ± SE	CV (%)
G1	29	26.8–30.9	28.1 ± 0.2	0.71	6	31.9–33.2	32.4 ± 0.2	0.62
G2	46	24.3–26.6	25.3 ± 0.1	0.40	60	25.9–31.0	28.0 ± 0.2	0.71
G3	51	22.1–24.2	23.1 ± 0.1	0.43	70	22.3–25.6	24.0 ± 0.1	0.42
G4	47	19.7–21.9	20.9 ± 0.1	0.48	50	19.3–22.0	20.9 ± 0.1	0.48
G5	33	17.0–19.6	18.5 ± 0.1	0.54	18	16.1–19.0	17.6 ± 0.2	1.14
G6	13	13.6–16.7	15.5 ± 0.3	1.94				

The units of P_n is μmol CO_2 m^{-2} s^{-1}.

observed values to the expected normally distributed values) showed that the P_n of the measured rice populations was normally distributed (Fig. 1-A and B). Normality tests using the Kolmogorov–Smirnov test also showed that the measured P_n data followed a normal distribution ($P = 0.936$ and 0.740 respectively).

Using K-means clustering, the A and B populations were clustered into five or six groups, and a significant difference in P_n was observed among the groups ($P < 0.05$). Table 1 shows the ranges, averages, and coefficients of variation for P_n in the six groups G1–G6, with photosynthetic rates shown from high to low. Variation in P_n was small within each group (Table 1), indicating that the clustered P_n groups were appropriate.

3.2. Photosynthetic patterns in the rice populations

The box diagram shows the variation in the main gas exchange parameters in each group in population A (Fig. 2). In each group, the variation in P_n was highest. For the other four parameters (g_s, CE, C_i and T_r), the variation was low, as was that among the groups. From G1 to G6, the variation in g_s decreased with P_n, whereas variation in CE was higher in the low and high P_n groups and lower in the intermediate group.

The photosynthetic groups were further clustered by K-means clustering. The photosynthetic groups in each population were divided into three clusters according to their differences in g_s and CE, namely the stomatal pattern (with higher g_s), the carboxylation pattern (with higher CE), and the intermediate pattern (with medium g_s and CE) (Table 2). The *F*-test showed no difference in P_n among the three types, but a significant difference in g_s and CE ($P < 0.01$), indicating that the classification was reliable. However, the proportion of each pattern differed between the two populations (Fig. 3) and among different P_n groups (Table 2).

3.3. Correlation analysis of P_n with g_s and CE

P_n was significantly correlated with g_s ($r = 0.810^{**}$ and 0.687^{**} in populations A and B) and CE ($r = 0.531^{**}$ and 0.933^{**} in population A and B) in both populations. The high correlation coefficients between P_n and CE indicate that photosynthetic rate was dominated by the carboxylation process in population B, whereas both stomatal and biochemical processes played an important role in P_n of population A.

The correlation coefficients were much higher when the three clusters with different photosynthetic patterns were examined (Fig. 4), particularly that between P_n and CE in population A (Fig. 4-B). This observation indicates that the classification of rice populations by the clustering method has biological meaning and is feasible.

4. Discussion

Correlation analysis is the most common method used to analyze gas exchange parameter data. P_n always correlates significantly with g_s [15,20]. A strong relationship between P_n and CE is also found during different wheat-growing periods [21] and among different soybean species [22]. In rice, previous reports also showed significant correlation both between P_n and g_s [5,23,24] and between P_n and CE [16,25,26]. In the present study, linear regression analysis showed significant correlations between P_n and g_s and between P_n and CE in both populations. However, the correlation coefficients differed between the two populations.

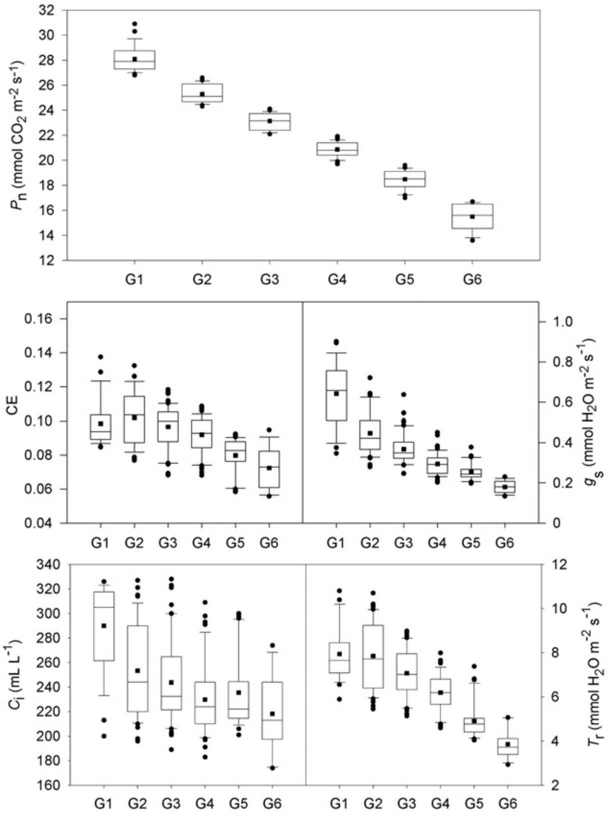

Fig. 2 – Variation of P_n, CE, g_s, C_i and T_r in the six groups in rice population A. ■ means of the data. ● discrete data points. Vertical boxes with error bars show the 10th, 25th, 50th, 75th and 90th percentiles of the data.

Table 2 – Photosynthetic patterns and their proportions in different photosynthetic rates (P_n) groups in populations A and B.

Group	Parameter	Cluster center						ANOVA			
		g_s pattern		CE pattern		Inter pattern		F-value		P-value	
		Pop. A	Pop. B	Pop. A	Pop. B	Pop. A	Pop. B	Pop. A	Pop. B	Pop. A	Pop. B
G1	P_n	28.28	32.90	27.45	32.20	27.62	32.60	1.34	0.708	0.28	0.56
	g_s	0.719	1.240	0.373	0.770	0.465	1.095	28.69	29.09	0	0.01
	CE	0.091	0.113	0.133	0.123	0.113	0.119	87.97	6.45	0	0.08
	Proportion (%)	72.41	16.67	6.90	50.00	20.69	33.33				
G2	P_n	25.39	27.90	25.47	26.90	25.10	28.30	1.13	1.39	0.33	0.26
	g_s	0.551	0.883	0.345	0.421	0.436	0.686	34.21	40.79	0	0
	CE	0.084	0.100	0.120	0.118	0.104	0.108	144.80	22.14	0	0
	Proportion (%)	32.61	46.67	28.27	5.00	39.13	48.33				
G3	P_n	23.15	23.80	23.12	24.20	23.17	24.10	0.018	0.585	0.98	0.56
	g_s	0.531	0.703	0.339	0.382	0.416	0.556	30.45	32.86	0	0
	CE	0.073	0.085	0.103	0.106	0.081	0.092	75.20	42.77	0	0
	Proportion (%)	7.84	34.29	74.51	5.71	17.65	60.00				
G4	P_n	21.13	20.90	20.83	20.90	20.79	21.00	0.737	0.06	0.48	0.94
	g_s	0.381	0.858	0.255	0.404	0.317	0.582	41.03	53.24	0	0
	CE	0.072	0.070	0.101	0.083	0.088	0.076	139.70	28.62	0	0
	Proportion (%)	12.77	8.00	48.94	50.00	38.30	42.00				
G5	P_n	18.06	17.70	18.56	16.10	19.60	17.60	2.41	1.62	0.11	0.23
	g_s	0.311	0.416	0.239	0.233	0.241	0.349	18.86	10.82	0	0
	CE	0.062	0.067	0.085	0.073	0.076	0.070	92.53	2.19	0	0.15
	Proportion (%)	21.21	55.56	75.76	5.56	3.03	38.88				
G6	P_n	15.00	–	15.30	–	15.83	–	0.77	–	0.49	–
	g_s	0.206	–	0.141	–	0.176	–	7.05	–	0.01	–
	CE	0.059	–	0.087	–	0.076	–	13.65	–	0	–
	Proportion (%)	30.77	–	15.38	–	53.85	–				

The units of P_n and g_s are μmol CO_2 m^{-2} s^{-1} and mmol H_2O m^{-2} s^{-1}, respectively.

The correlation in population A between P_n and g_s was much higher than that between P_n and CE. There was a very high positive correlation between P_n and CE in population B. These differing relationships indicate several physiological differences in the photosynthesis of the two populations.

When correlation analyses are based on a large number of species, correlation coefficients are often very low, although always significant. For example, in a study of 54 species of wheat [27], the highest correlation coefficient between P_n and g_s during three different periods was only 0.4365. In a study of 12 soybean species [28], the relationship between P_n and g_s differed during different growth periods. The relationship between P_n and g_s at the flowering stage showed a cubic polynomial curve fit, while at the later filling stage, it showed a linear fit ($R^2 = 0.68$). In the present study, when correlations were calculated for three different photosynthetic patterns, significantly higher correlations were observed between P_n and g_s or CE in each pattern (Fig. 4). These correlations were much stronger than those for the whole population. Notably, the correlation between P_n and CE in population A was only 0.531, whereas the lowest correlation was 0.828 among the three photosynthetic patterns (Fig. 4-B). These data indicate that the real correlation between P_n and other gas exchange parameters in rice is concealed by differences in the physiological patterns of photosynthesis.

The two rice populations were divided into three clusters with different photosynthetic patterns according to differences in gas exchange parameters: the stomatal pattern, carboxylation pattern, and intermediate pattern. However, the proportions of the three photosynthetic patterns differed between the two populations. In population B, P_n was highly positively correlated with CE, but the CE pattern was shared by only 17.65% of the population. This finding indicates that P_n was limited by lower CE in this population. NPT was developed at the IRRI with the aim of increasing the yield potential of rice by 2%–25% [29,30]. However, the yield potential of NPT rice is limited by its lower photosynthetic rate [31–33]. Hu et al. [23] showed that lower stomatal frequency and higher stomatal resistance are the main constraints on the photosynthetic rate of rice NPT lines. Our results showed that both g_s and CE improved in the group with the highest P_n following a cross with wild rice (Table 3).

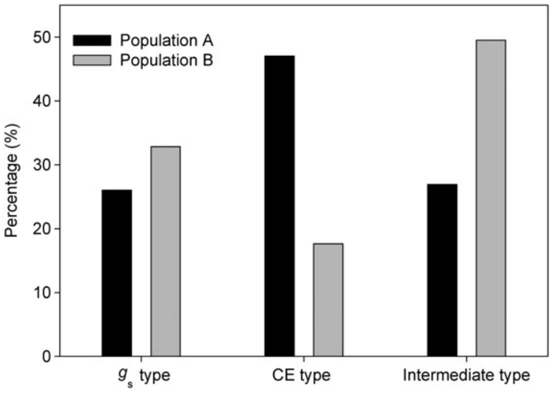

Fig. 3 – Proportions of three photosynthetic patterns in two rice populations.

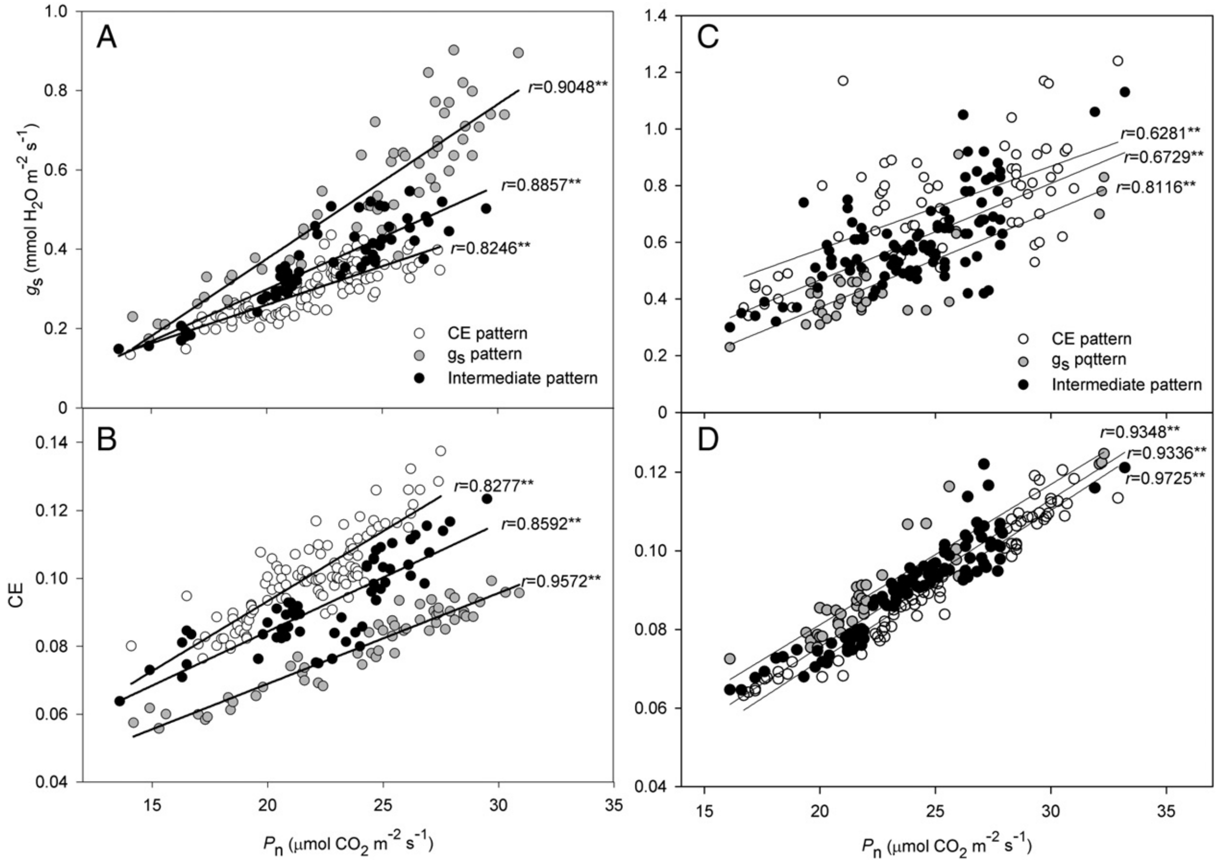

Fig. 4 – Correlation analysis of P_n with g_s (A, C) and CE (B, D) in the three clusters with different photosynthetic patterns in rice populations A (A and B) and B (C and D).

In fact, g_s was improved in this population, but its improvement did not result in an increase in P_n, owing to weak improvement in CE. Both g_s and CE were generally improved in population A. Perhaps without the backcrossing, the population maintained more of the diversity contributed by the cross with sorghum.

Our results will help guide the breeding of rice with high photosynthetic rates. Crossing rice lines with either the stomatal or carboxylation pattern will produce rice progeny with both high g_s and high CE, and thus a high P_n. This strategy will make the increase in breeding efficiency more evident. But given that photosynthesis is sensitive to environmental stress, another question is which pattern is most beneficial to crops for overcoming stress and maintaining higher photosynthesis. The answer awaits further studies of the response of rice plants with different photosynthetic patterns to various environmental stresses.

Table 3 – P_n, g_s and CE of the six plants in the group with highest photosynthetic rate (P_n) in rice population B.

Photosynthetic patterns	P_n (μmol m^{-2} s^{-1})	g_s (mmol m^{-2} s^{-1})	CE
g_s pattern	32.9	1.240	0.1134
CE pattern	32.1	0.697	0.1221
	32.3	0.830	0.1247
	32.2	0.782	0.1224
Intermediate pattern	33.2	1.130	0.1212
	31.9	1.060	0.1160

5. Conclusions

Rice populations were divided by K-means clustering into three physiological patterns based on differences in gas exchange parameters. Higher correlation coefficients were observed between P_n and g_s or CE in each cluster than in the full population. This finding indicates that clustering is very important for understanding factors limiting rice photosynthesis.

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