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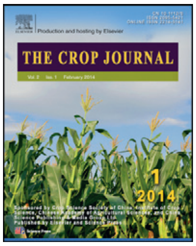

Three photosynthetic patterns characterized by cluster analysis of gas exchange data in two rice populations

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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

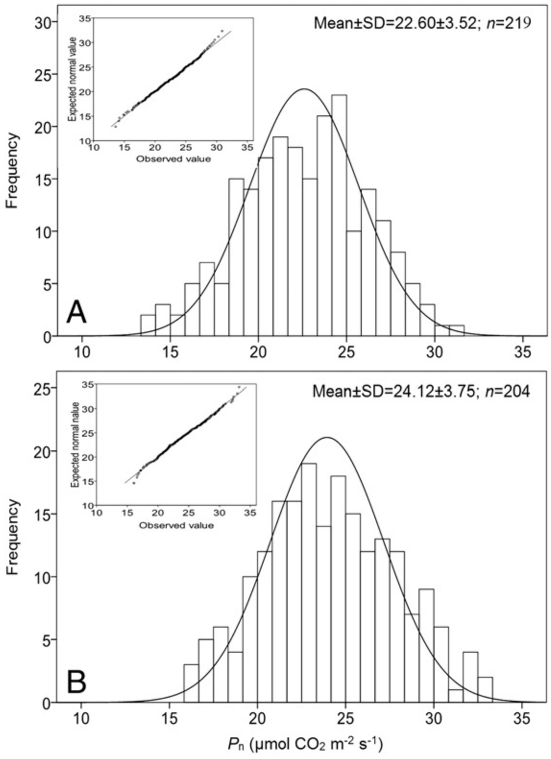

Fig. 1 – Normal distribution of net photosynthetic rate in rice populations A and B. The main plot shows the histogram and the inset shows the Q–Q plot of P_n. In population A, the P_n values of the two parents are 25.5 ($YF_{2\text{-}1}$) and 41.4 (Shennong 133) μmol CO_2 m^{-2} s^{-1}; in population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