BRIEF COMMUNICATION

Determinant of photosynthetic capacity in rice leaves under ambient air conditions

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Abstract

At the grain-filling stage, net photosynthetic rate (P_N), stomatal conductance (g_s), and ribulose-1,5-bisphosphate carboxylation efficiency (CE) were correlated in order to find the determinant of photosynthetic capacity in rice leaves. For a flag leaf, P_N in leaf middle region was higher than in its upper region, and leaf basal region had the lowest P_N value. The differences in g_s and CE were similar. P_N, g_s, and CE gradually declined from upper to basal leaves, showing a leaf position gradient. The correlation coefficient between P_N and CE was much higher than that between P_N and g_s in both cases, and P_N was negatively correlated with intercellular CO_2 concentration (C_i). Hence the carboxylation activity or activated amount of ribulose-1,5-bisphosphate carboxylase/oxygenase rather than g_s was the determinant of the photosynthetic capacity in rice leaves. In addition, in flag leaves of different tillers P_N was positively correlated with g_s, but negatively correlated with C_i. Thus g_s is not the determinant of the photosynthetic capacity in rice leaves.

Additional key words: carboxylation efficiency; flag leaf; intercellular CO_2 concentration; leaf position; net photosynthetic rate; *Oryza*; stomatal conductance.

Net photosynthetic rate (P_N) in plant leaf is often influenced by environment factors such as irradiance, temperature, and water supply, and also by leaf age, leaf position, and developmental stage. The findings on the changes in P_N, g_s, and ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) content during leaf development are summarized in Šesták (1985) and Čatský and Šesták (1997). However, the question remains what is the determinant of the differences in P_N between leaves of different age, different position, and different regions of a leaf. We tried to solve these questions using a correlation analysis.

Rice (*Oryza sativa* L. hybrid combination GD-1S/RB207) plants were grown in the experimental field of China National Hybrid Rice Research and Development Center (Changsha, Mapoling). They were managed using common culture techniques for the region. P_N was measured when rice plants were at the filling stage. During 10:00–16:00 (Beijing time) P_N in attached flag leaves was measured *in situ* at saturating irradiance, air CO_2 concentration of 350 µmol mol^{-1}, and air temperature of 30 °C using a portable infrared gas analysis system *LI-6400* (*Li-Cor*, USA). The irradiation source provided by *LI-6400* was used to supply irradiance saturating photosynthesis, about 1 200 µmol(photon) m^{-2} s^{-1}. CE was measured using a set of CO_2 concentrations from 250 to 50 µmol mol^{-1}, decreasing by 50 µmol mol^{-1}. About two minutes were required to stay at each CO_2 concentration before P_N value was recorded. The *Sigma Plot 6.0* software was used to analyze experiment data and make correlation analysis.

The measured flag leaves were about 60 cm long and their basal, middle, and top regions were about 10, 30, and 50 cm from their leaf sheath, respectively. P_N in different regions of flag leaf was significantly different. The middle and basal region showed the highest and the lowest value, respectively (Fig. 1*A*). And there were similar differences in g_s and CE between the different regions

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Abbreviations: C_i – intercellular CO_2 concentration; CE – carboxylation efficiency; g_s – stomatal conductance; P_N – net photosynthetic rate.
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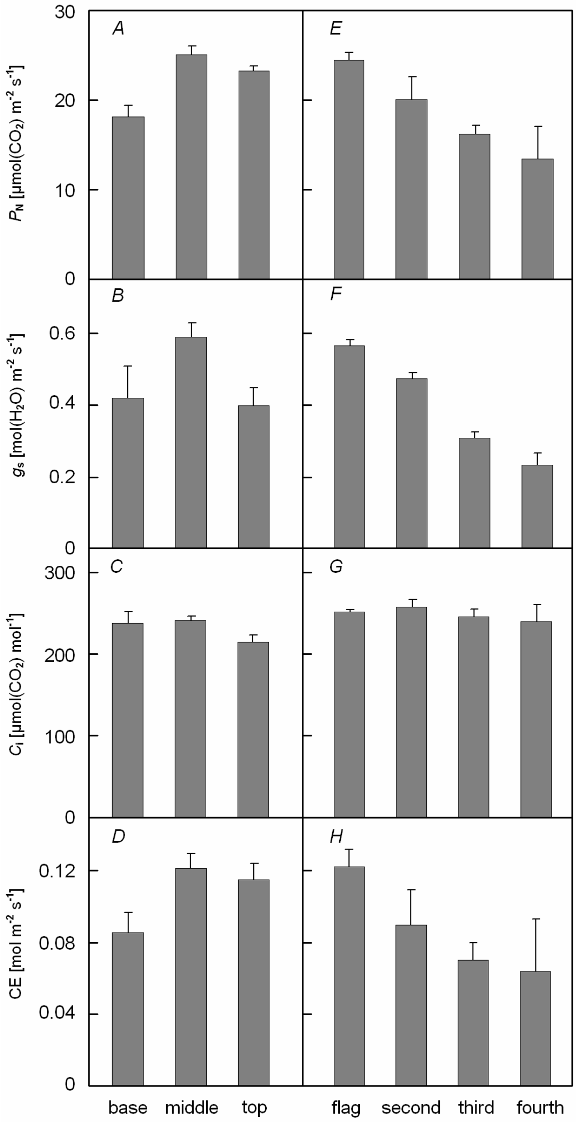

Fig. 1. Net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), and carboxylation efficiency (CE) in rice leaves of different regions (*left*) and position (*right*).

(Fig. 1*B*, *D*). Correlation analysis indicated that the correlation coefficient between P_N and CE was much higher (Fig. 2*A*, $r^2 = 0.86$) than that (Fig. 2*B*, $r^2 = 0.21$) between P_N and g_s, and P_N was negatively correlated with C_i (Fig. 2*C*).

In leaves of different position P_N was also different. The flag leaf had the highest P_N value which gradually declined with lowering of leaf position (Fig. 1*E*). Also there were similar differences in g_s and CE (Fig. 1*F*, *H*). The correlation coefficient between P_N and CE was much higher (Fig. 2*D*, $r^2 = 0.94$) than that (Fig. 2*E*, $r^2 = 0.56$) between P_N and g_s, and P_N was negatively correlated with C_i (Fig. 2*F*).

In one socket of a side line of the experimental field there were two rice plants totally having 35 tillers. Among the flag leaves of these tillers the highest P_N value was 22.4 µmol(CO_2) m^{-2} s^{-1} and the lowest one was 9.29 µmol(CO_2) m^{-2} s^{-1}. P_N values of the other leaves were within 14–21 µmol(CO_2) m^{-2} s^{-1}. The mean of all these leaves was 15.8±0.5 µmol(CO_2) m^{-2} s^{-1}. In addition, similar results were obtained when 40 flag leaves of a side line were randomly measured: The highest P_N was 22.9 µmol(CO_2) m^{-2} s^{-1} and the lowest one was 17.3 µmol(CO_2) m^{-2} s^{-1}. P_N values of the other leaves were within 18–22 µmol(CO_2) m^{-2} s^{-1}. The mean value for the 40 leaves was 19.7±0.2 µmol(CO_2) m^{-2} s^{-1} and higher than that of the 35 tiller flag leaves mentioned above. This difference may be due to that those shorter tillers, which have commonly lower P_N, were not measured deliberately.

The results of correlation analysis of the above data showed that P_N was positively correlated with g_s, but negatively correlated with C_i (Fig. 2*G*,*H*), implying that g_s is not the determinant of P_N difference among the flag leaves of different tillers.

Our results about P_N differences between different leaf regions and between rice leaves of different position indicate that the determinant of leaf photosynthetic capacity is RuBP carboxylation activity rather than g_s though high P_N is always accompanied by high g_s and they are always positively correlated with each other. The following facts support this conclusion: (*1*) High P_N was always accompanied by high CE (Fig. 1) and CE was positively correlated with carboxylation activity or activated amount of RuBPCO (Farquhar *et al.* 1980, Cammerer and Farquhar 1981, Farquhar and Sharkey 1982). (*2*) The correlation coefficient of P_N with CE was much higher than that of P_N with g_s (Fig. 2). (*3*) P_N was negatively correlated with C_i (Fig. 2). If g_s was the determinant of the photosynthetic capacity, P_N should be positively correlated with C_i. However, it is not true. Because CE values in the flag leaves of different tillers were not compared, we can not state if carboxylation activity or active amount of RuBPCO is also the determinant of the difference in the photosynthetic capacity between the flag leaves of different tillers. The fact that P_N was negatively correlated with C_i (Fig. 2), however, favours the conclusion that g_s is not the determinant of the difference in the photosynthetic capacity.

As high P_N was always accompanied by high CE in wheat (Yang *et al.* 1999), soybean (Jiang and Xu 2001), rice (Chen *et al.* 2002, Jiang and Xu 2002), the conclusion presented above may have universal importance. Moreover, this conclusion is also consistent with the universally accepted viewpoint that RuBPCO is the key limiting step in photosynthetic carbon assimilation (Jensen 2000, Bernacchi *et al.* 2001). The difference in RuBPCO content is likely related to different development stages and/or different irradiances during leaf development. Among leaves of different position, for example, the flag leaf is the latest to appear and to senesce and is located at the top of plant. So it can obtain more

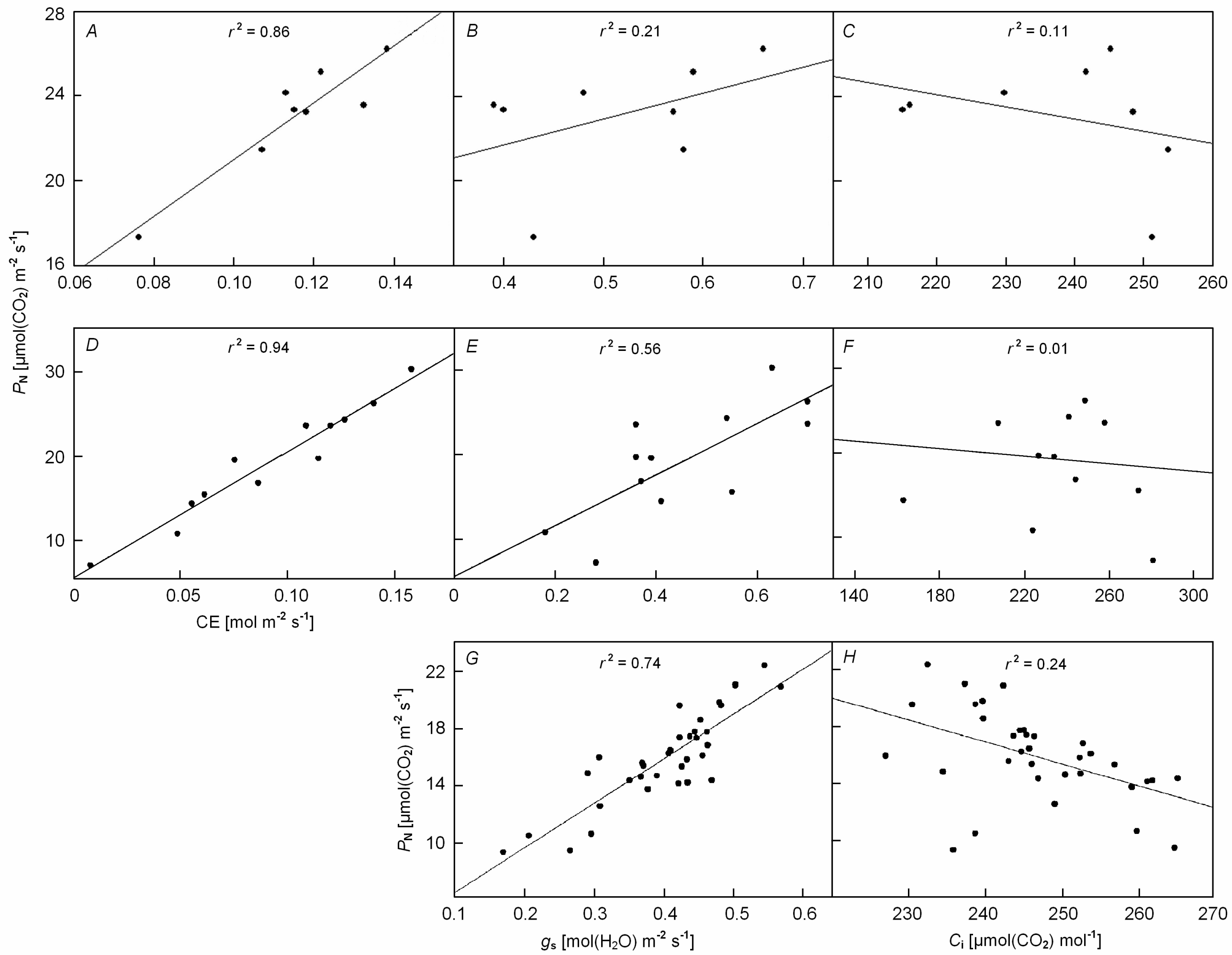

Fig. 2. The correlation of net photosynthetic rate (P_N) with carboxylation efficiency (CE), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) in different regions of flag leaf (*A*–*C*), leaves of different position (*D*–*F*), and different tiller flag leaves of one socket leaf (*G*–*H*).

photon energy during development and is less old in development, having higher RuBPCO content and carboxylation activities and greater photosynthetic capacity than all other leaves. Murchie *et al.* (2002) reported that the irradiation-saturated P_N and the amount of RuBPCO per unit leaf area in rice leaves rose with increasing irradiance during leaf growth and declined with lowering leaf position in canopy. Their results support our deduction.

Because of significant differences in P_N between leaves of different position, leaves of different tillers, and different leaf regions, it is very important to choose leaves similar in position, orientation, age, region of leaf blade, and irradiation environment when P_N is compared between different cultivars or hybrid combinations.

References

Bernacchi, C.J., Singsaas, E.L., Pimentel, C., Portis, A.R., Long, S.P.: Improved temperature response functions for models of Rubisco-limited photosynthesis. – Plant Cell Environ. **24**: 253-259, 2001.

Caemmerer, S. von, Farquhar, G.D.: Some relationship between the biochemistry of photosynthesis and the gas exchange of leaves. – Planta **153**:376-387, 1981.

Čatský, J., Šesták, Z.: Photosynthesis during leaf development. – In: Pessarakli, M. (ed.): Handbook of Photosynthesis. Pp. 633-660. Marcel Dekker, New York – Basel – Hong Kong 1997.

Chen, Y., Wang, X.-H., Liao, Y., Cai, S.-Q., Zhang, H.-B., Xu, D.-Q.: [Effect of flag leaf orientation on its photosynthetic capacity in rice.] – J. Plant Physiol. mol. Biol. **28**: 396-398, 2002. [In Chin.]

Farquhar, G.D., Caemmerer, S. von, Berry, J.A.: A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. – Planta **149**: 78-90, 1980.

Farquhar, G.D., Sharkey, T.D.: Stomatal conductance and photosynthesis. – Annu. Rev. Plant Physiol. **33**: 317-345,

1982.
Jensen, R.G.: Activation of Rubisco regulates photosynthesis at high temperature and CO_2. – Proc. nat. Acad. Sci. USA **97**: 12937-12938, 2000.
Jiang, H., Wang, X.-H., Deng, Q.-Y., Yuan, L.-P., Xu, D.-Q.: Comparison of some photosynthetic characters between two hybrid rice combinations differing in yield potential. – Photosynthetica **40**: 133-137, 2002.
Jiang, H., Xu, D.-Q.: The cause of the difference in leaf net photosynthetic rate between two soybean cultivars. – Photosynthetica **39**: 453-459, 2001.
Murchie, E.H., Hubbart, S., Chen, Y., Peng, S., Horton, P.: Acclimation of rice photosynthesis to irradiance under field conditions. – Plant Physiol. **130**: 1999-2010, 2002.
Šesták, Z. (ed.): Photosynthesis During Leaf Development. – Academia, Praha; Dr W. Junk Publ., Dordrecht – Boston – Lancaster 1985.
Yang, Q.-F., Jiang, H., Xu, D.-Q.: [Changes in photosynthetic efficiency of flag leaves of wheat during development.] – Acta phytophysiol. sin. **25**: 408-412, 1999. [In Chin.]