Short Report

Rice Leaf Photosynthesis as a Function of Nitrogen Content and Crop Developmental Stage*

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発育ステージを考慮した水稻の光合成速度と葉身窒素含有量の関係式 : 長谷川利拡・堀江 武** (九州東海大学農学部・**京都大学農学部)

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Higher leaf nitrogen per unit leaf area (NA) promotes higher photosynthetic rates and greater radiation use efficiency of rice (*Oryza sativa* L.)⁹⁾. Both photosynthesis and radiation use efficiency decrease as the plant matures^{2,3)}, and as the structural components of the leaf increase and NA decreases. However, the photosynthetic decline with crop age is not only a consequence of NA^{10,12)} but is also influenced by the level of rubisco⁷⁾ as well as the stomatal aperture⁶⁾. In order to analyze the effects of N on rice productivity all through the growing period, it is necessary to understand the quantitative relation between photosynthesis and NA in relation to the crop developmental stage. The present study is an investigation of the extent to which the photosynthetic decline in rice can be accounted for by a simple empirical model based on NA and a developmental index, DVI, which is a continuous variable representing the crop developmental stage⁴⁾. A model was developed from data derived from an experiment covering a wide range of N supply to the plant.

Materials and Methods

Circulating flow water culture was conducted in a glass house at Kyushu Tokai University in 1990. The size of the culture bed was 0.64 m × 3.9m (4 rows × 16 hills, 26 hills m⁻²) with a 700 l solution tank. Cultivar Nipponbare was sown on May 15 and transplanted on the culture bed on June 14. We had four levels of N ; 1, 3, 5, and 30 ppm and the concentrations of other nutrients were same for all the treatments, similar to those used by Toriyama et al.¹³⁾. Culture solution was replaced weekly and pH was adjusted to 5.1 every morning. The net photosynthetic

rate, Pn, was measured six times during the growing period (Jul. 8, 25, Aug. 13, 24, Sep. 10 and Oct. 4) when PAR was more than 1600 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ by a portable leaf photosynthesis apparatus (LI-6200, Li-Cor). Three fully developed leaves from the top of four undisturbed plants randomly chosen from the two central rows were selected for the measurement. After the measurement, leaf area, dry weight and Kjeldahl N were determined. The DVI is a function of air temperature and day length set so that DVI=0 at emergence, 1 at panicle initiation, 2 at heading and 3 at maturity.

Results and Discussion

Figure 1 shows the relation between Pn and NA. In this study, NA ranged from 0.5 to 1.9 gm⁻². Correlation between Pn and NA was highly significant ($P < 0.001$) but relatively low ($r = 0.72$), indicating that the model accounted for only about 50% of the variation in the data. One of the major sources of variance was the sampling stage. The Pn decreased with DVI even without a decline in NA.

The following logistic function suggested by Sinclair and Horie⁹⁾ expresses well the relationship at each sampling stage ;

$$Pn = P_{\max} (2 / (1 + \exp(-a(NA - N_0))) - 1) \quad (1)$$

where, a is a slope and N_0 is specific leaf N when $Pn = 0$, respectively. The $P_{\max}$ is the maximum value for Pn that decreased gradually with DVI. This change was formulated as follows ;

$$P_{\max} = P_m \exp(-b \text{ DVI}) \quad (2)$$

where, b and P_m are parameters.

Equation (1) combined with Eq.(2) was fitted to the data by means of the Simplex algorithm¹⁾. The function explains a large part of the variation in Pn due to NA and DVI with

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Fig. 1. The relation between net photosynthetic rates, P_n , and leaf N content on a leaf area basis, N_A .

□ DVI=0.73, ■ DVI=1.12, ○ DVI=1.78,
● DVI=2.15, △ DVI=2.55, ▲ DVI=3.00.

four parameters ($r=0.862$, $SE=2.82 \mu\text{mol m}^{-2}\text{s}^{-1}$). The optimal solutions for each parameter were $38.4 \mu\text{mol m}^{-2}\text{s}^{-1}$ for P_m , $1.40 \text{ gN}^{-1}\text{m}^2$ for a , 0.282 for b and 0.252 g m^{-2} for N_0 . The estimated parameters indicated that at each N_A , P_n would decrease by 10% at heading and by 40% at maturity relative to that at panicle formation.

Assuming that the leaf dark respiration rate per unit leaf area is expressed as a function of leaf temperature (T) as $2.72 \times 2.0^{(T/10-3)} \mu\text{mol m}^{-2}\text{s}^{-1}$ after Horie²⁾, we obtain gross photosynthesis, P_g . The parameters estimated for P_g were $43.4 \mu\text{mol m}^{-2}\text{s}^{-1}$ for P_m , 1.19 for a , 0.230 for b and 0.0369 g m^{-2} for N_0 . The r value was increased slightly to 0.879 .

There is no a priori reason that N_0 remains constant. We therefore estimated N_0 's specifically for each sampling date. The estimated N_0 's ranged from 0.034 to 0.399 for P_n and from -0.09 to 0.16 for P_g . The r value improved only modestly by 0.028 for P_n and by 0.020 for P_g though the model had five additional parameters. We therefore concluded that N_0 does not have a strong influence on goodness of fit and could be treated as a constant parameter over developmental stages.

Several factors are involved in the change in the relation between photosynthetic rates and

N_A . First, N_A does not necessarily represent the variation in the amount and the activity of photosynthetic enzymes such as rubisco during senescence⁸⁾, which is the major determinant of photosynthetic rates⁷⁾. Secondly, sensitivity of the response of stomatal aperture to stress decreases with age independently of changes in the N status of the leaves^{5,6)}. This could cause a decline in the value of parameter P_{max} . There is also the possibility that the photosynthetic rate could be influenced by a large amount of accumulated photosynthate in leaves¹⁵⁾ and the altered sink:source ratio¹⁴⁾. In addition, leaf water status largely affects the relationship¹¹⁾. The present model was derived empirically and does not explain all the variation caused by these factors. Nevertheless, the model does account for 76 ~ 77% of the experimental variation ($r=0.86$ ~ 0.88) and so can be used in a crop growth model to take into account the effects of N over developmental stages.

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