Relationship between Leaf Photosynthesis and Nitrogen Content of Field-Grown Rice in Tropics

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ABSTRACT

A field-derived relationship between maximum single leaf net photosynthetic rate under saturating light (A_{max}) and leaf N content per unit leaf area (N_a) is not available for rice (*Oryza sativa* L.). The rice simulation model ORYZA1 estimates aboveground dry matter production based on the relationship between A_{max} and N_a determined previously under greenhouse-growth chamber conditions. The objectives of this study were to establish to relationship between A_{max} and N_a under field conditions and to determine whether the field-derived relationship could improve ORYZA1 estimation of aboveground dry matter production of tropical irrigated rice. Rice plants were grown in the field with different N rates in the 1993 dry season. The A_{max} and N_a were determined at 38 and 88 d after transplanting. Aboveground dry matter was determined at physiological maturity. Dry matter production data at physiological maturity from four other field experiments were used for model evaluation. There was a close correlation between A_{max} and N_a under field conditions ($r^2 = 0.88$). Compared with the relationship between A_{max} and N_a as determined under greenhouse-growth chamber conditions in previous studies, higher A_{max} was observed at low N_a in this field study. When the field-derived relationship between A_{max} and N_a was used, ORYZA1 estimation of dry matter production was improved for rice grown in tropical irrigated environments.

T HERE IS a close relationship between maximum leaf photosynthetic rate under saturating light (A_{max}) and leaf N content in many plant species (Field and Mooney, 1986). This relationship has been reported to be linear or curvilinear in different studies on rice. Mitsui and Ishii (1938, 1939) first reported that A_{max} was linearly correlated with leaf N concentration per unit dry weight (N_{dw}) between 32.6 and 64.2 g N kg^{-1} ($r = 0.84$). Other studies also reported a linear relationship between A_{max} and leaf N content per unit leaf area (N_a) (Osada, 1967; Yoshida and Coronel, 1976; Uchida et al., 1982; Cook and Evans, 1983a; Makino et al., 1988). On the other hand, a curvilinear relation between A_{max} and N_a was reported by Murata (1961), Takano and Tsunoda (1971), and Cook and Evans (1983b) in rice lines with diverse genetic origins. In these studies, a linear relationship between A_{max} and N_a was found below 1.6 g N m^{-2}, but A_{max} leveled off above 1.6 g N m^{-2}.

A rice simulation model for irrigated ecosystems, ORYZA1, was developed jointly by the Int. Rice Research Inst. (IRRI) and Wageningen Agricultural Univ. (Kropff et al., 1994). In this model, A_{max} is calculated from N_a and average daytime air temperature. Daily CO$_2$ assimilation of the canopy is calculated based on A_{max}, leaf N profile in the canopy, light distribution in the canopy, and leaf area index. The net daily crop growth rate is obtained from daily CO$_2$ assimilation after subtracting respiration requirements. The ORYZA1 (Version 1) underestimates dry matter production of tropical irrigated rice when the observed dry matter production is low. Low dry matter production is often caused by low solar radiation, such as in the wet season, and low leaf N content at later growth stages.

It is hypothesized that the greenhouse-derived relationship between A_{max} and N_a is mainly responsible for the underestimation with ORYZA1 of dry matter production. The relationship between A_{max} and N_a used in the ORYZA1 was established based on data from many species, such as beet (*Beta vulgaris* L.), rice, soybean [Glycine max (L.) Merr.], and wheat (*Triticum aestivum* L.) (van Keulen and Seligman, 1987). Most studies on the relationship between A_{max} and leaf N were based on pot-grown plants with soil or culture solution under greenhouse-growth chamber conditions, and A_{max} was often determined under artificial light provided by incandescent lamps (Nevins and Loomis, 1970; Yoshida and Coronel, 1976; Cook and Evans, 1983a; Evans, 1983; Makino et al., 1988). Field conditions in the tropics, however, differ greatly from greenhouse or chamber environments in terms of light level and quality, temperature, and humidity. These may cause different growth and development characteristics between plants grown in the field and in the greenhouse-growth chambers. In this study, we measured A_{max} and N_a of field-grown rice plants with a portable photosynthesis system. The objectives of this study were to determine the relationship between A_{max} and N_a under tropical field conditions and to test whether the field-derived relationship could improve ORYZA1 estimation of dry matter production of tropical irrigated rice.

MATERIALS AND METHODS

A field experiment was conducted in the 1993 dry season (January–April) at the IRRI, Los Baños, Philippines. The soil was an Andaqueptic Haplaquoll with pH 6.0, 16.2 g organic C kg^{-1}, 1.5 g total N kg^{-1}, and 32.9 cmol kg^{-1} cation-exchange capacity. Treatments were arranged in a split-plot design with four replicates. Main plots were different N fertilizer levels and subplots consisted of either the indica inbred IR72 or a new tropical indica F$_1$ hybrid IR64616H (Table 1). Nitrogen levels were 0, 45, 120, 165, 180, and 225 kg ha^{-1} as prilled urea. All plots received 18 kg P ha^{-1} as single superphosphate and 33 kg K ha^{-1} as KCl incorporated before transplanting. Fourteen-day-old seedlings were transplanted on 12 Jan. at a hill spacing of 0.2 by 0.2 m with five plants per hill. Subplot dimensions were 5 by 6 m.

Single leaf net photosynthetic rates were measured with a portable photosynthesis system (LI-6200, LI-COR, Lincoln, NE). To ensure light saturation, A_{max} was measured between

Table 1. Field experiments conducted in the International Rice Research Institute (IRRI), Los Baños, Laguna, and the Philippine Rice Research Institute (PhilRice), Muñoz, Nueva Ecija, the Philippines.

Year	Season	Location	Variety	Fertilizer N level
				——— kg ha^{-1} ———
1991	Wet	IRRI	IR72, IR59109-113-3-3-2	0, 80, 110
1992	Dry	IRRI	IR72, IR59109-113-3-3-2, IR64616H	0, 100, 180, 225
1992	Wet	IRRI	IR72, IR58185-23-3-3-1, IR64616H	0, 30, 80, 110
1993	Dry	IRRI	IR72, IR64616H	0, 45, 120, 165, 180, 225
1993	Dry	PhilRice	IR72, IR64616H	0, 45, 120, 165, 180, 225

1000 and 1300 h at 38 and 88 d after transplanting (DAT) when the photosynthetically active photon flux (PAR) was between 1800 and 2000 µmol m^{-2} s^{-1}. A 0.25-L chamber was used to enclose the middle portion of the uppermost fully expanded leaf. Four leaves from each plot of three replicates were selected for the measurements. The gas exchange system was operated as a closed system to measure photosynthetic rate during a 20-s period. After the measurement of A_{max}, the leaf was detached and area, dry weight, and total N were determined for each entire leaf blade. Area was measured with a leaf area meter (LI-3000, LI-COR). Dry weight was determined after oven-drying at 70°C to constant weight. Total leaf N was determined on the entire leaf blade by micro Kjeldahl digestion and distillation (Bremner and Mulvaney, 1982). Leaf N content was expressed on a leaf area basis.

A rice stimulation model, ORYZA1 (Kropff et al., 1994), was used to simulate aboveground dry matter production of varieties and N fertilizer levels in five field experiments (Table 1). The four other field experiments had the same experimental design as the experiment conducted in the 1993 dry season at IRRI. Grain yield was determined from a 5-m^2 harvest area at physiological maturity. Harvest index was determined from a 0.5-m^2 harvest area at the same time as grain yield. Aboveground dry matter production was calculated from grain yield and harvest index. Separate simulations were run with the regression equations between A_{max} and N_a reported by van Keulen and Seligman (1987) or as derived from this study. The input requirements of the model were daily weather data (total radiation and minimum and maximum air temperatures), plant spacing, and date of crop emergence and transplanting. The simulated dry matter production was compared with actual values by linear correlation.

RESULTS AND DISCUSSION

The relationship between A_{max} and N_a was not significantly different from IR72 and IR64616H at 38 and 88 DAT. Therefore, all data were pooled in Fig. 1. There was a close correlation between A_{max} and N_a. The A_{max} was linearly related to N_a within the observed range of N_a:

$$A_{max} = 6.00 + 14.20N_a \qquad [1]$$

van Keulen and Seligman (1987) reported a generic relationship between A_{max} and N_a based on the data from beet, rice, maize, and wheat:

$$A_{max} = -4.10 + 20.45N_a \qquad [2]$$

Equation [2] is similar to the equations of Yoshida and Coronel (1976) and Makino et al. (1988) for rice (Fig. 2). Most studies indicated a linear relationship when N_a
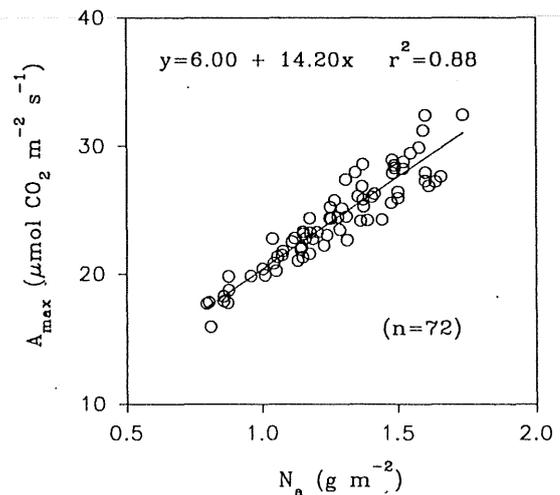
Fig. 1. Relationship between light-saturated single leaf photosynthetic rate (A_{max}) and leaf N content on a leaf area basis (N_a) of IR72 and IR64616H at 38 and 88 d after transplanting, 1993 dry season, at Int. Rice Research Inst., Los Baños, Philippines. Each data point is the mean of four subsamples.

ranges from 0.5 to 2.1 g m^{-2}. The curvilinear response used by Sinclair and Horie (1989) was based on the data of Takano and Tsunoda (1971) in which A and N_a were determined on 40 rice lines from diverse genetic origins. This curvilinear relationship might have resulted from growth limitations in some of the genotypes by factors other than leaf N, which in turn may have influenced the relationship between A_{max} and N_a.

Most of the studies on the relationship between A_{max} and N_a were conducted in pots with soil or solution-culture systems under greenhouse–growth chamber conditions (Table 2), probably due to unavailability of a portable photosynthesis system. The relationship be-
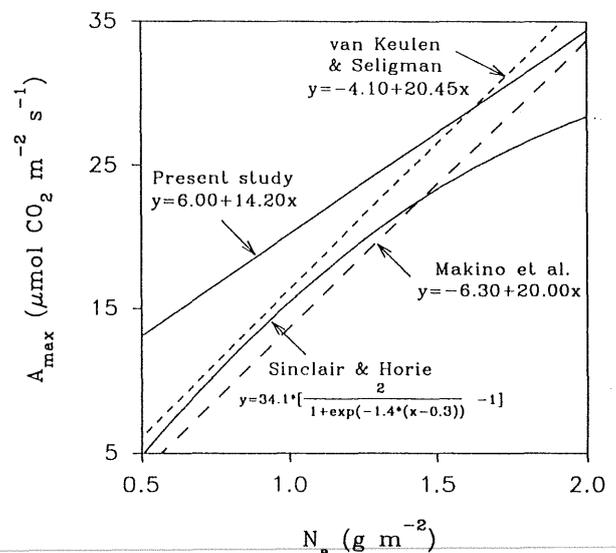
Fig. 2. Comparison of relationships between light-saturated single leaf photosynthetic rate (A_{max}) and leaf N content on a leaf area basis (N_a) reported by van Keulen and Seligman (1987), Makino et al. (1988), and Sinclair and Horie (1989) and determined in this study.

Table 2. Cultural conditions of rice plants, light level, and light source when photosynthetic rates were measured for the studies on the relationship between photosynthetic rate and leaf N content.

Author	Year	Culture conditions	Light level	Light source
Mitsui and Ishii	1938	greenhouse, solution	−†	—
Mitsui and Ishii	1939	pot with soil	27 klux (527)‡	—
Murata	1961	solution	50 klux (977)	—
Osada	1967	solution	45 klux (879)	—
Takano and Tsunoda	1971	greenhouse, soil	85 klux (1660)	incandescent lamps
Yoshida and Coronel	1976	solution	−	—
Uchida et al.	1982	greenhouse, solution	70 klux (1367)	—
Cook and Evans	1983a	phytotron, soil	800§	incandescent lamps
Makino et al.	1988	phytotron, solution	1800§	incandescent lamps
Present study	1994	field	1800-2000§	full sunlight

† Information not available.

‡ Only illumination unit (kilolux) was provided. Numbers in parentheses were converted from kilolux to μmol photon $m^{-2} s^{-1}$ [photosynthetically active photon flux (PAR)] assuming 1 klux = 19.53 μmol photon $m^{-2} s^{-1}$.

§ μmol photon $m^{-2} s^{-1}$ (PAR).

tween A_{max} and N_a determined under tropical field conditions in this study was different from previously reported relationships (Fig. 2). The field-derived equation indicates a higher A_{max} at low leaf N values, especially at $N_a < 1$ g m^{-2} compared with other equations. In the 1992 dry season, A_{max} and N_a were measured on 16 flag leaves at mid-grain filling. Average N_a was 1.00 ± 0.03 (standard deviation) g m^{-2} and average A_{max} was 19.5 ± 0.8 μmol $m^{-2} s^{-1}$. Calculated A_{max} based on Eq. [1] was 20.2, which was close to the observed value. Calculated A_{max} based on Eq. [2] was 16.4, which was 16% lower than the observed value. The discrepancy between Eq. [1] and [2] may be due to the differences in species and/ or in plant growth and development caused by different light levels and quality, temperature, and humidity between greenhouse-growth chamber and tropical field conditions. Potted plants may also grow differently from field-grown plants because of root restriction. Gas exchange measurement techniques were previously not available or not adaptable to permit accurate determination of leaf photosynthetic rate under field conditions. Within the past few years, stable and miniature infrared CO_2 gas analyzers have been developed and incorporated into portable photosynthesis systems such as the LI-6200 used in this study. Although Eq. [1] was based on data from only one season, photosynthesis measurements were determined on 288 leaves (means of four subsamples were used in Fig. 1) of two varieties at two growth stages. Relationships between A_{max} and N_a reported ear-

lier were based on only a few data points determined at one growth stage.

Aboveground dry matter production of treatments in the five field experiments were separately simulated with ORYZA1 using Eq. [1] and [2]. With both equations, the model accurately estimated dry matter production in treatments that had dry matter accumulation >15 t ha^{-1} (Table 3). In contrast, both simulation models underestimated dry matter in the treatments with dry matter accumulation <15 t ha^{-1}, but the estimation was improved by using Eq. [1] compared with Eq. [2] (Table 3; Fig. 3). With Eq. [2], ORYZA1 underestimated dry matter by 10% but only by 2% with Eq. [1]. Average canopy N_a of treatments with low dry matter levels was generally lower than that with high dry matter levels (e.g., 1.1 vs. 1.3 g N m^{-2} at flowering in the 1992 dry season experiment). Therefore, using the greenhouse-derived equation between A_{max} and N_a underestimates A_{max} of low N leaves of field-grown rice plants in the tropical environments and results in greater underestimation of

Table 3. Observed and simulated dry matter production of five field experiments (Table 1) using the rice simulation model ORYZA1. The regression equations between light saturated single leaf photosynthetic rate (A_{max}) and leaf N content on a leaf area basis (N_a) developed by van Keulen and Seligman (1987) and derived from this study were used in the ORYZA1, respectively.

Group	Number of observations	Observed value	Simulated with Eq. [1]†	Simulated with Eq. [2]†
			t ha^{-1}	
Less than 15 t ha^{-1}	30	9.9	9.7 (−2)‡	8.9 (−10)
More than 15 t ha^{-1}	24	17.6	17.9 (2)	17.6 (0)

† Equation [1] = relationship between A_{max} and N_a derived from this study; Equation [2] = relationship between A_{max} and N_a developed by van Keulen and Seligman (1987).

‡ Numbers in parentheses are the percentages of difference from the observed value.
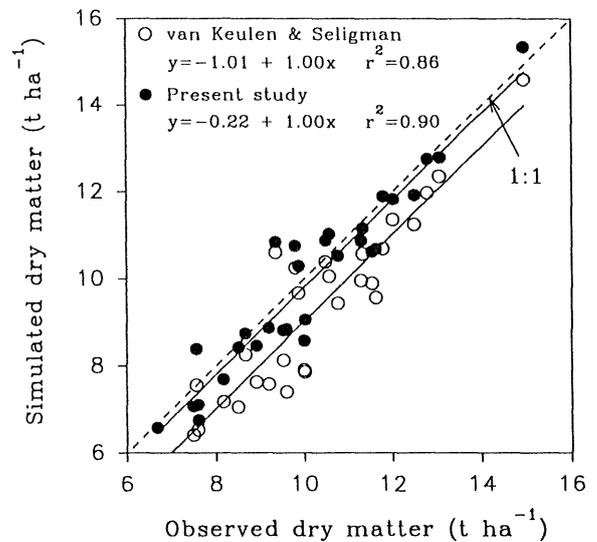
Fig. 3. Comparison between observed (<15 t ha^{-1}) and simulated aboveground dry matter production of treatments in five field experiments (Table 1) with the rice simulation model ORYZA1. The regression equations between light-saturated single leaf photosynthetic rate (A_{max}) and leaf N content on a leaf area basis (N_a) developed by van Keulen and Seligman (1987) and derived from this study were used in the ORYZA1 simulations.

dry matter production of tropical irrigated rice by the simulation model ORYZA1 than when the equation is used that was developed in this study.

In conclusion, the field-derived relationship between A_{max} and N_a of tropical irrigated rice was significantly different from those previously determined under greenhouse-growth chamber conditions, especially in the low N_a range. The field-derived relationship improves the estimation of dry matter production of tropical irrigated rice by the rice simulation model ORYZA1.

ACKNOWLEDGMENTS

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