

## Planting pattern affects the rate of photosynthesis during ripening in rice plants

Yumiko San-oh<sup>1</sup>, Taiichiro Ookawa and Tadashi Hirasawa

Faculty of Agriculture, Tokyo University of Agriculture and Technology, Fuchu, Tokyo 183-8509, Japan.

[www.tuat.ac.jp](http://www.tuat.ac.jp)

<sup>1</sup>Corresponding author : [rice@cc.tuat.ac.jp](mailto:rice@cc.tuat.ac.jp)

### Abstract

A planting pattern in which each hill contains one rice plant (planting pattern I) results in a higher yield of dry matter, especially during the reproductive stage, than a planting pattern in which each hill contains three plants (planting pattern III). Plants in planting pattern I maintain a higher rate of leaf photosynthesis during senescence in the ripening stage, which may contribute in part to the higher yield of dry matter in these plants. We found close linear relationships between the ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) content and the rate of photosynthesis, as well as between leaf contents of nitrogen and Rubisco during the ripening stage. These relationships were independent of planting pattern and the position of a leaf on the stem. Thus, plants in planting pattern I maintained a higher rate of photosynthesis and also contained a higher level of Rubisco than plants in planting pattern III. Plants in planting pattern I could keep the higher content of leaf nitrogen due to their higher capacity of nitrogen accumulation than plants in planting pattern III. This may contribute to the higher content of leaf Rubisco which, in turn, is associated with a higher rate of photosynthesis.

### Media summary

Planting a single rice plant per hill results in a higher rate of photosynthesis during ripening because of the higher contents of nitrogen and, subsequently, Rubisco in a leaf.

### Key Words

Direct-sown plants, Nitrogen accumulation, Nitrogen content, Photosynthesis, Rubisco, Senescence.

### Introduction

Rice planted in such a manner that each hill contains one plant (planting pattern I) produces a heavier dry matter than rice planted so that each hills contains three plants (planting pattern III). This effect was noted in both transplanted and direct-sown plants and was most pronounced during the reproductive stage (San-oh et al. 2004). The higher yield of dry matter is associated with the production of heavier grains in these plants (Table 1). Planting pattern I results in a canopy that consists of more erect leaves and the extinction coefficient of the canopy is smaller for these plants than for those in planting pattern III. In addition, plants in planting pattern I maintain a higher leaf chlorophyll content during ripening when compared to plants in planting pattern III. Delayed leaf senescence is considered an important factor in the production of heavier dry matter and heavier grain. It was observed in many crops that the rate of leaf photosynthesis was kept high during the ripening stage, and heavier dry matter and heavier grain were produced in the plants with slower leaf senescence (e.g. Jiang et al. 1988). In this paper, we compared the rate of photosynthesis and the characteristics related to photosynthesis during leaf senescence between planting patterns I and III for direct-sown rice plants in a submerged paddy field.

### Materials and Methods

#### *Materials and cultivation of plants*

Rice plants (*Oryza sativa* L. cv. Takanari) were grown in the paddy field of the University Farm (30° 41' N latitude, 139° 29' E longitude) in alluvial soil (clay loam). Plants were sown on May 1, 2002 and were grown at a density of 51.3 (15 cm × 13 cm) hills m<sup>-2</sup> with one plant per hill (planting pattern I) and at a

density of 17.5 (30 cm × 19 cm) hills m<sup>-2</sup> with three plants per hill (planting pattern III). As a basal dressing, manure was applied at a rate of about 2 kg m<sup>-2</sup> and chemical fertilizer was applied at the rate of 5.0, 5.0 and 5.0 g m<sup>-2</sup> for N, P<sub>2</sub>O<sub>5</sub> and K<sub>2</sub>O, respectively. Topdressing was applied at the rate of 3.0 g each per m<sup>2</sup> for N and K<sub>2</sub>O on July 23, and August 21. Heading (50% heading) occurred on August 12. Plants were harvested on October 12. The experiment was designed with three randomly arranged replicates (28 m<sup>2</sup> for each replicate).

#### *Measurements of the rate of photosynthesis and the diffusion conductance*

The rate of photosynthesis and diffusion conductance were measured with a portable photosynthesis system (LI-6400; LI-COR Inc.) in leaves attached to the main stem. The quantum flux at a leaf surface, relative humidity and flow rate in the chamber, and leaf temperature were controlled to 2,000 μmol m<sup>-2</sup> s<sup>-1</sup>, 60-70 %, 180 μmol s<sup>-1</sup> and 30 °C, respectively. After the rate of photosynthesis was measured at an ambient concentration of CO<sub>2</sub> of 350 μl l<sup>-1</sup>, the rate was measured at an intercellular concentration of CO<sub>2</sub> of 270 μl l<sup>-1</sup>.

#### *Measurements of the ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and nitrogen levels in leaves*

Rubisco was measured by the single radial immuno-diffusion method of Sugiyama and Hirayama (1983) with rabbit polyclonal antibodies raised against purified Rubisco from rice. Nitrogen concentration was determined with a CN analyzer (MT-600; Yanaco Inc., Kyoto, Japan), and nitrogen content was calculated as the product of the dry weight and the nitrogen concentration.

**Table 1 Comparison of dry matter accumulation, grain yield and harvest index in direct-sown plants with different planting patterns.**

Year	Dry weight		Yield		Harvest index	
	(kg m <sup>-2</sup> )		(g m <sup>-2</sup> )		(% )	
	I	III	I	III	I	III
2001	2.27 a	1.86 b	971 a	861 b	40.0 a	38.6 b
2002	2.17 a	1.87 b	936 a	813 b	36.0 a	37.8 a
2003	2.15 a	1.74 b	941 a	731 b	39.7 a	39.0 a

I and III represent the planting pattern I and III (see text), respectively. Means followed by different letters are significantly different at the 5% level by LSD (least significant difference) test (n=3). Dry weight of aboveground parts at harvest. Yield is given for water content of 14.5%. Harvest index was calculated by dividing the dry weight of brown rice by the dry weight of aboveground parts.

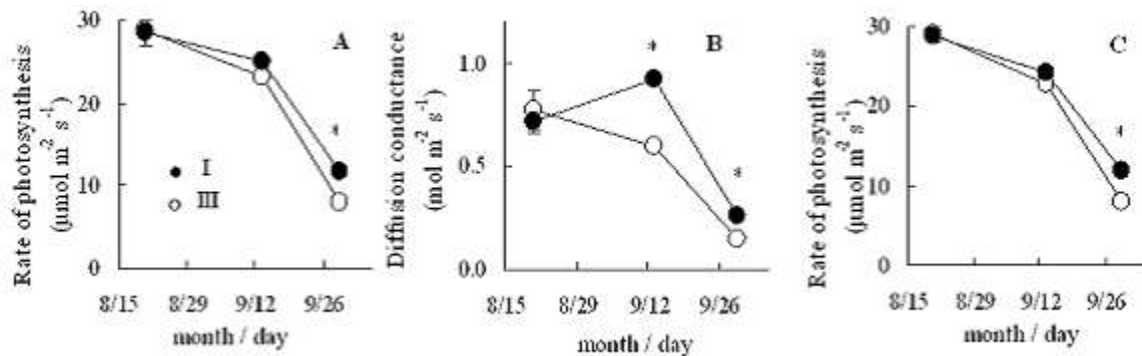
## **Results**

#### *Rate of photosynthesis and diffusion conductance*

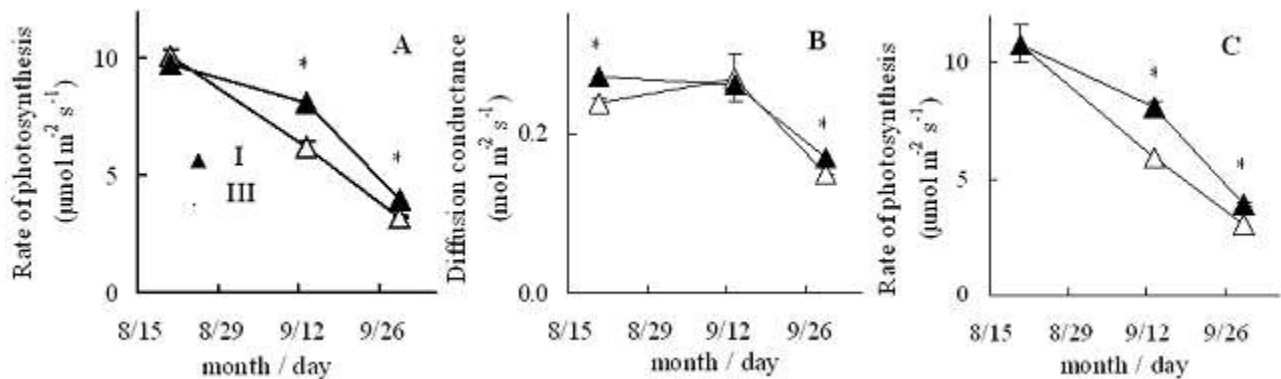
At the early (Aug. 15-17) and middle (Sep. 12-14) ripening stage, the rate of photosynthesis at an ambient concentration of CO<sub>2</sub> of 350 μl l<sup>-1</sup> in the flag leaf was similar for plants in either planting pattern I

or III (Fig. 1 A). However, at the late ripening stage (Oct. 3-6), the rate of photosynthesis was higher in plants in planting pattern I. In addition, the diffusion conductance was larger in these plants at the middle and late ripening stages (Fig. 1 B). The differences in the rate of photosynthesis at an intercellular CO<sub>2</sub> concentration of 270  $\mu\text{l l}^{-1}$  were similar to those at an ambient CO<sub>2</sub> concentration of 350  $\mu\text{l l}^{-1}$  (Fig. 1 A, C).

There were no differences between plants in the rate of photosynthesis at an ambient concentration of CO<sub>2</sub> of 350  $\mu\text{l l}^{-1}$  for the fourth leaf at the early ripening stage (Fig. 2 A). Thereafter, the rates were higher in plants in planting pattern I. Although some differences in the diffusion conductance were observed between the plants (Fig. 2 B), the differences in the rate of photosynthesis at an intercellular CO<sub>2</sub> concentration of 270  $\mu\text{l l}^{-1}$  were similar to those at an ambient CO<sub>2</sub> concentration of 350  $\mu\text{l l}^{-1}$  (Fig. 2 A, C). These results indicate that the leaf photosynthetic activity is responsible in part for the difference in the rate of photosynthesis at an ambient CO<sub>2</sub> concentration of 350  $\mu\text{l l}^{-1}$ .



**Fig. 1** Changes in the rate of photosynthesis (A, C) and diffusion conductance (B) of a flag leaf. Closed and open circles represent plants in planting pattern I and III, respectively. A: Measurements at an ambient CO<sub>2</sub> concentration of 350  $\mu\text{l l}^{-1}$ . C: Measurements at intercellular CO<sub>2</sub> concentration of 270  $\mu\text{l l}^{-1}$ . Vertical bars represent standard deviation (n=2). \* Values are significantly different at 5% level (t-test).

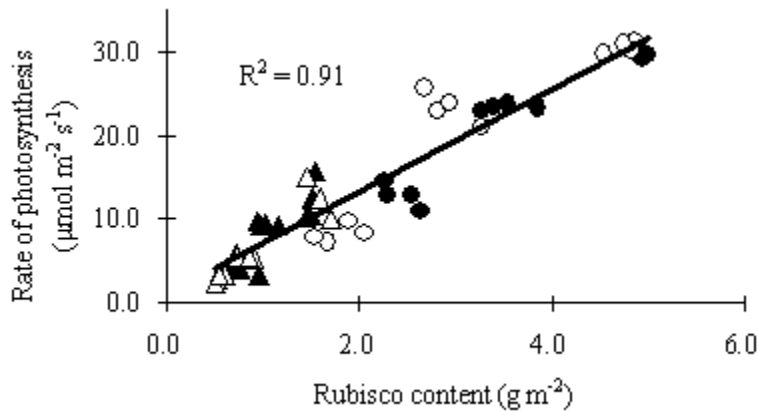


**Fig. 2** Changes in the rate of photosynthesis (A, C) and diffusion conductance (B) of a fourth leaf. Closed and open triangles represent plants in planting pattern I and III, respectively. A: Measurements at an ambient CO<sub>2</sub> concentration of 350  $\mu\text{l l}^{-1}$ . C: Measurements at intercellular CO<sub>2</sub> concentration of 270  $\mu\text{l l}^{-1}$ . Vertical bars represent standard deviation (n=2). \* Values are significantly different at 5% level (t-test).

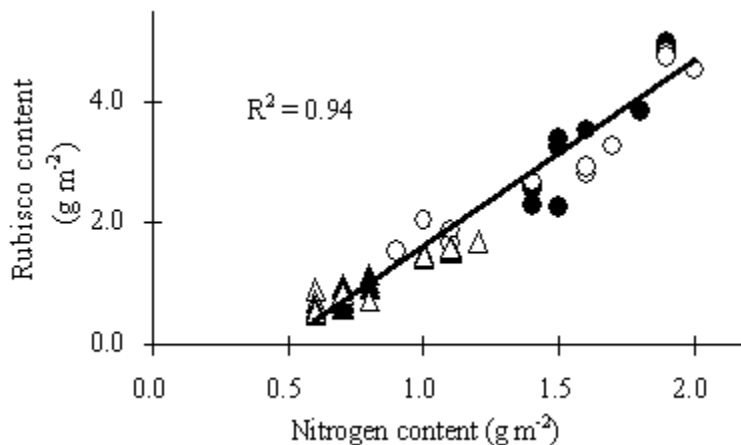
#### *Relationships between contents of Rubisco and nitrogen and the rate of photosynthesis*

A close linear relationship between the Rubisco content and the rate of photosynthesis was observed which was independent of planting pattern and the position of a leaf on the stem (Fig. 3). The nitrogen

and Rubisco contents (Fig. 4) correlated linearly and were also independent of planting pattern and leaf position. The plants in planting pattern I accumulated more nitrogen than plants in planting pattern III; however, there was no difference in the apparent partitioning of nitrogen to leaves between the plants (data not shown).



**Fig. 3** Relationship between Rubisco content and the rate of photosynthesis\*. \*The rate of photosynthesis at the intercellular CO<sub>2</sub> concentration of 270 μl l<sup>-1</sup>. Circles and triangles represent the flag leaf and the 4th leaf, respectively. Closed and open symbols represent the plants in planting pattern I and III, respectively.



**Fig. 4** Relationship between nitrogen content and Rubisco content. Circles and triangles represent the flag leaf and the 4th leaf, respectively. Closed and open symbols represent the plants in planting pattern I and III, respectively.

## Conclusion

Rice plants in planting pattern I maintained a higher rate of photosynthesis during ripening than the plants in planting pattern III. The higher rate of photosynthesis was the result of higher contents of nitrogen and, consequently, Rubisco in the leaves of these plants. The higher nitrogen content in the leaves of plants in planting pattern I resulted mainly from a higher level of nitrogen accumulation. These characteristics may contribute to the higher yield of dry matter in plants in planting pattern I compared to plants in planting pattern III.

## References

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