Cultivation and Ecophysiology of Rice Plants in the Tropics*

III. Photosynthesis of rice cultivars of India, measured by the Tsuno's simple method

Tetsuro TANIYAMA, S.V. SUBBAIAH**, M.L.N. RAO**
and Katsuhiko IKEDA

(Faculty of Bioresources, Mie University, Tsu, 514, Japan,

** Directorate of Rice Research, Rajendranagar, Hyderabad
500 030 A.P., India)

Received January 22, 1987

Abstract : Photosynthetic activities of four rice cultivars of India was investigated by employing a new method devised by Tsuno¹⁰⁾. The improved cultivars Vijayamahsuri, Sonamahsuri, HR 35 and HR 59 and the local scented cultivar Basmati were used.

The temperature optimum for photosynthesis was found to be 38°C in all cultivars in the experiment done by the new method. Cultivars Vijayamahsuri and Sonamahsuri had a relatively high ability to photosynthesize under low light intensities. The chlorophyll content of the leaves affected significantly the rate of CO₂ uptake. Photosynthetic activity of the leaf differed not only with the cultivar but also with its position on the culm. At the ripening stage the flag leaf in cvs. Vijayamahsuri and HR 35 showed the highest photosynthetic capacity, whereas in cv. Sonamahsuri the second and third leaf assimilated greater amounts of CO₂ than the flag leaf did. A close correlation was found between the chlorophyll content and the photosynthetic ability of the leaf, when pooled for all the upper three leaves of four cultivars, except for the case of leaves in cv. HR 59 with only a slight difference in chlorophyll content.

We considered that the method devised by Tsuno¹⁰⁾ and newly introduced here will be available for the test of photosynthetic activity of crop plant, especially for the researches dealing with a great number of materials.

Key words : Chlorophyll content, Leaf position on the stem, Method for measurement of photosynthesis, *Oryza sativa*, L., Photosynthetic capacity.

熱帯地域における稲作およびその生態生理学的研究 第3報 簡易光合成測定法によるインド栽培水稻の光合成速度：谷山鉄郎・S.V. スバイヤ*・M.L. ナラシマ・ラオ*・池田勝彦（三重大学生物資源学部・インド国立稲作総合研究所）

要 旨：津野^{10,11)}によって考案された簡易光合成測定法をインド、ハイデラバード地方における栽培水稻の光合成測定に応用した。実験材料には、Vijayamahsuri, Sonamahsuri, Basmati, HR 59 および HR 35 を用いた。Vijayamahsuri はアンドラプラデッシュ州の、また Sonamahsuri はインド国立稲作総合研究所の奨励品種である。香り米の Basmati は市場価格も高く、アラブ諸国への輸出用として栽培されている。これらの栽培品種はインド・デカン高原で手植えの慣行法で栽培されていた。光合成測定には、慣行法で栽培されていた水稻の完全展開の葉身中央部約12cm²を用いた。光源は自然光とし、光合成測定と共に葉緑素含量も測定した。CO₂飽和水を用いた温度—光合成曲線より最適温度は日本型水稻^{10,11)}と同じ38°Cであった。改良品種の Sonamahsuri と Vijayamahsuri は在来品種の Basmati に比較して光合成速度が高かった。また、改良品種は弱光域における光利用効率が高かった。光飽和点は改良および在来品種ともに約20 klxであった。CO₂飽和水の交換によって、光合成速度は再び高い値を示した。各葉位の光合成速度は葉緑素含量と密接な関係にあった。また、光合成速度と葉緑素含量との間には高い正の相関関係が見られた。簡易光合成測定法は、簡便で、安価で、しかも測定精度が高く、現場で容易に適用しうることから、赤外線ガス分析計等の測器の整備困難な事情のもとでの測定法として大いに役立つものと思われる。

キーワード：イネ、光合成測定法、光合成能力、葉位、葉緑素含量。

Photosynthesis is a primary factor determin-

ing rice production. Attention has been paid on the varietal differences in photosynthetic activity in rice plants^{1,2,3,6,8)}. Generally, the rate of photosynthesis per unit leaf area in japonica rice varied with cultivar by some 20% from the average. Ohno⁵⁾ had reported that relative-

* This part of research is collaborative work of Japan Society for the Promotion of Science and Indian National Science Academy. A part of this work was presented at the 181st Meeting of the Crop Science Society of Japan, April, 1986.

ly great differences in the rate of photosynthesis were found among indica cultivars grown at the IRRI, some of them being higher in the rate of photosynthesis than the others by 30% and that eight varieties of indica rice with a very high photosynthetic efficiency could be selected out of 301 varieties examined. Such cultivars seem to be of great value in breeding program, but the measurement as well as the identification of the photosynthetic rate of a large number of cultivars is difficult, because their activities should be evaluated precisely and compared with each other under the same conditions. It was also reported that some indica rices showed higher net assimilation rates than japonica ones, and that the partial contribution of net photosynthetic rate to dry matter production was about 30%, whereas that of the leaves was about 70% of the total dry matter production⁵). It is interesting whether or not any difference in the rate of photosynthesis of leaves exists between japonica and indica rice cultivars.

A number of reports^{2,3,4,6,7,8,9}) concerned with the photosynthesis of rice leaves have been published mainly on the japonica cultivars. These data may be principally applicable to the indica cultivars too, but this needs to be ascertained in more detail. Photosynthetic rate of leaves can be determined by measuring the rate of either CO₂ uptake or O₂ evolution. Usually the amounts of CO₂ uptake was measured by employing the infra-red gas analyzer. The O₂ evolution from the leaves can also be used as an indicator for photosynthetic rate, by which dissolved O₂ into the solution can be detected and measured by utilizing the oxygen electrode. Recently, Tsuno¹⁰) has developed a very simple method for measurement of photosynthesis.

The present study was carried out to secure the information on apparent photosynthetic rates of leaves in some rice cultivars of India at different growth stages and it is the first experiment that is conducted in the open field by employing the Tsuno's method for the determination of the photosynthetic rates of the rice of India.

Materials and Methods

Materials used here were rice cultivars of India, Vijayamahsuri, Sonamahsuri, HR 35,

HR 59 and Basmati; the former three cultivars are the improved and the latter one the local scented type.

Apparent photosynthesis was estimated by the method developed by Tsuno^{10,11}). This method is very simple in construction and the instrument has been modified from Pycnometer. In the present experiment, 2 litre volume beaker was used as a water-bath. To hold test-tubes upright in a beaker, wires were stretched crosswise. The 35-ml volume test-tubes were filled with CO₂-saturated water through which great quantities of the expired air was passed for about 5 min. Excised leaf-blade with about 12 cm² in area was inserted in the test-tube. Ensuring that no air bubbles existed, these tubes were then connected with 1-ml scaled pipette via silicon stopper. These test-tubes were kept in the dark for 15 min, by covering with two layers of black vinyl-film, so as to prevent the light penetration as well as to keep the temperature of both leaf and CO₂-saturated water at 38°C. Immediately after the removal of vinyl covers the initial readings of the pipette were recorded. After 10 min. exposure to sunlight, the readings of the pipette were recorded again and differences between both readings were obtained. All experiments, including the blank (control) without leaf, were repeated for 3 times. Throughout the experiment water temperature in a beaker was kept at about 38°C, by pouring a small quantity of hot water into the water-bath at appropriate intervals. The photosynthetic rate was calculated by the following formula proposed by Tsuno¹⁰):

$$Y = 6.74X + 3.89$$

where, Y is the amount of CO₂ absorbed by the leaves and expressed in mg · dm⁻² · hr⁻¹. X is the volume of water increased with the exhausted gas from leaves and expressed in ml H₂O · dm⁻² · hr⁻¹. Intensities of solar radiation on the horizontal plane were measured by the Lux Meter (Toshiba No.5 type) at requisite time when photosynthesis was examined. In the experiments to determine light-photosynthesis curves of the cultivars, solar radiation increased with time from early in the morning to 10:00 local standard time (LST) on fine days.

The chlorophyll content was estimated by using standard formula:

$$C = 3.7 (a - 0.33)$$

where, C is the chlorophyll content expressed in $\text{mg} \cdot \text{dm}^{-2}$ and a is the reading of Fuji Green Meter (GM 1).

Results and Discussion

Photosynthetic rates of the rice cultivars of India were examined at different stages of crop growth and the results are summarized in Figs. 1 to 6. Fig. 1 shows the temperature-photosynthesis curves of four rice cultivars growing at the early tillering stage, when measured by varying the temperature of CO_2 -saturated water in which excised leaf-blade was inserted. Temperature for maximizing the photosynthetic rate was found to be 38°C , the optimum temperature for photosynthesis being quite the same in all cultivars. In contrast to the high photosynthetic capacity in cvs. Sonamahsuri, Vijayamahsuri and HR 59, cv. Basmati showed a relatively low photosynthetic rate at temperatures ranging from 18° to 40°C . Chlorophyll content of leaf-blades estimated just before the examination was as low as $2.51 \text{ mg} \cdot \text{dm}^{-2}$ in cv. Basmati, whereas those of cvs. Sonamahsuri, Vijayamahsuri and HR 59 were 3.78 , 3.34 and $3.27 \text{ mg} \cdot \text{dm}^{-2}$, respectively. Then, the low rate of photosynthesis in cv. Basmati could be ascribable in part to a low content of chlorophyll in the leaf. It is also of interest that cv. HR 59, a scented type, showed still high activity in photosynthesis even at a temperature as high as 43°C during the early growth stage.

The light-photosynthesis curves at the maximum tillering stage are given in Fig. 2. It is apparent that the photosynthetic activities increased rectilinearly with increasing light intensity in every cultivar. Among cultivars examined, Sonamahsuri and Vijayamahsuri, as compared with Basmati and HR 59, showed not only high photosynthetic ability under light saturation, but also high efficiency in solar energy utilization even under lower light intensities. The light saturation points obtained here were 20 klx in all cultivars tested, being a considerably low value beyond expectation. The cause for this could be explained as follows: Light intensities were measured at horizontal plane, despite of a lower solar elevation in the morning, and the excised leaf materials in a test-tube were held upright. Accordingly, actual intensities of the light received by leaf-blades were much higher

than those shown on the abscissa of the Fig. 2.

This figure also shows that the photosynthetic rate of cv. Basmati was higher than that of cv. HR 59, being different from the results given in Fig. 1. Since the chlorophyll content of which leaves were determined for their photosynthesis was higher in cv. Basmati ($2.80 \text{ mg} \cdot \text{dm}^{-2}$) than in cv. HR 59 ($2.38 \text{ mg} \cdot$

Fig. 1. Changes in apparent photosynthesis as affected by temperature in rice cultivars of India at early active tillering stage. Apparent photosynthesis rate is expressed as the estimated value computed from the Tsuno's method and the temperature given in the figure is that of the water saturated with CO_2 , into which test leaf was immersed.

Fig. 2. Relation between apparent photosynthesis and light intensity in rice cultivars of India at maximum tillering stage.

Fig. 3. Changes in apparent photosynthetic rate of the upper three leaves of cv. HR 59 at the early ripening stage.

Symbols Δ , $\circ$ and $\times$ denote the flag, the second and third leaf, respectively. The arrows in the figure denote the time of the exchange of CO_2 -saturated water.

Fig. 4. Changes in apparent photosynthetic rate of the upper three leaves of cv. Vijayamahsuri at the ripening stage. For details, refer to Fig. 3.

Fig. 5. Changes in apparent photosynthetic rate of the upper three leaves of cv. HR 35 at the heading stage. For details, refer to Fig. 3.

Fig. 6. Changes in apparent photosynthetic rate of the upper three leaves of cv. Sonamahsuri at the ripening stage. For details, refer to Fig. 3.

dm^{-2}), the cause of this discrepancy between their photosynthetic capacities can be attributed chiefly to the chlorophyll content in leaves, rather than to the difference in the growth stage.

Photosynthesis in rice population is the summation of photosynthesis of individual leaves. At the ripening stage, especially, the upper three leaves of rice plant have an important role for grain filling. Chlorophyll content of their blades, needless to say, has a decisive effect on the photosynthetic activity. In cv. HR 59, the chlorophyll contents of the flag, the second and third leaf at the early ripening stage were 2.48, 2.37 and 2.15 $\text{mg} \cdot \text{dm}^{-2}$, respectively.

Fig. 3 represents the changes in the photosynthetic ability of the upper three leaves in cv. HR 59 with time of day. The light intensity during 09:25 to 11:35 LST fluctuated between 45 and 62 klx, but the water in a beaker was kept at constant temperature of 38°C. Comparing with the photosynthetic rate of the upper three leaves immediately after the exchange of water saturated with CO_2 , the second or third leaf always assimilated greater amounts of CO_2 than the flag leaf, giving the maximum value of 34 $\text{mg} \cdot \text{dm}^{-2} \cdot \text{hr}^{-1}$ with the second leaf at 11:15 LST. Although the second and third leaves showed a higher photosynthetic rate than the flag leaf, no significant difference in chlorophyll content was found among the leaves of cv. HR 59. Therefore, we considered that the difference in photosynthetic ability with leaf position was

not merely ascribable to chlorophyll content of the leaf in the case of cv. HR 59.

The changes in photosynthetic capacity in cv. Vijayamahsuri growing at the ripening stage was examined on a sunny day, the light intensity fluctuating between 60 and 88 klx. The amounts of CO_2 uptake were measured at 20 min. intervals after the exchange of water saturated with CO_2 . Results obtained are shown in Fig. 4. Chlorophyll contents of the upper three leaves counted from the top were 3.52, 3.22 and 2.78 $\text{mg} \cdot \text{dm}^{-2}$, respectively. In cv. Vijayamahsuri the flag leaf assimilated the greatest amount of CO_2 , followed by the second and then the third leaf when measured at 10:20 LST, differing from those of cv. HR 59. This clearly indicates that the high content of chlorophyll in the leaf is important for cv. Vijayamahsuri to assimilate much more amounts of CO_2 . Immediately after the exchange of CO_2 -saturated water, the CO_2 uptake in cv. Vijayamahsuri increased with greater rapidity, comparing with the other cultivars used.

In order to examine the photosynthetic ability of improved cultivar HR 35, a local photoperiod-insensitive type with fine grains, the characteristics of CO_2 uptake at 38°C was studied. As seen from Fig. 5, the flag leaf with the highest content of chlorophyll (3.18 $\text{mg} \cdot \text{dm}^{-2}$) assimilated greater amounts of CO_2 (47 $\text{mg} \cdot \text{dm}^{-2} \cdot \text{hr}^{-1}$) in comparison with those of the other two leaves. This trend was similar to that observed in cv. Vijayamahsuri.

Photosynthetic rates of cv. Sonamahsuri

growing at the ripening stage were investigated under the irradiance of 80 to 95 klx and the results are given in Fig. 6. The trend of photosynthesis of this cultivar was somewhat different from that of cvs. Vijayamahsuri and HR 35. It was the second leaf that assimilated the greatest amount of CO_2 , showing the maximum value of $42.4 \text{ mg} \cdot \text{dm}^{-2} \cdot \text{hr}^{-1}$ around noon. Among the upper three leaves, the second one had the highest concentration of chlorophyll ($3.40 \text{ mg} \cdot \text{dm}^{-2}$) and the concentration decreased to $3.18 \text{ mg} \cdot \text{dm}^{-2}$ of the third leaf and followed by the flag one ($3.03 \text{ mg} \cdot \text{dm}^{-2}$). It seemed that the difference in the photosynthetic rate among the leaves was closely related with the chlorophyll content of the leaf, but not with the leaf position on the stem.

Fig. 7 illustrates the relationship between chlorophyll contents and the apparent photosynthesis of upper three leaves in all cultivars used. The photosynthesis clearly increased with the increase in chlorophyll content, giving a highly significant correlation coefficient. Thus, we came to the conclusion that the chlorophyll content of the leaves closely related to the CO_2 uptake ability in high yielding cultivars at least, and that low rates of

photosynthesis of the leaves obtained with cv. HR 59, a scented type, were mainly due to low content of chlorophyll. Throughout a day, relatively high activities of photosynthetic CO_2 uptake were found with cvs. Sonamahsuri and Vijayamahsuri. Since the amounts of CO_2 uptake by the leaf changes with light intensity which fluctuates during day, a greater variation in photosynthetic rate will occur, if more number of cultivars are tested.

A sharp increase in CO_2 uptake by the leaf did occur when exposed to the light for 10 min. just after the second exchange of CO_2 -saturated water, exceeding that of the first one. This phenomenon was always observed with all cultivars used in the present study, excepting the second and third leaf of cv. HR 59. Tsuno¹⁰ reported, however, that japonica rice cultivars were able to assimilate a great amount of CO_2 with only the first 10 min. exposure to sunlight and then followed by a gradual decrease in CO_2 uptake. The method employed in the present study was slightly different from that of Tsuno¹⁰. We measured CO_2 uptake with excised leaves by exchanging CO_2 -saturated water at about one hour intervals. A slight difference in the method used will cause the data obtained to differ. However, it is possible to compare with the photosynthetic activity of different cultivars each other. The Tsuno's method is very simple and applicable and makes it possible to measure the photosynthetic rate of a vast number of materials with great rapidity and accuracy.

Acknowledgements

We wish to express our thanks to Dr. J.E. Shinde, Project Director, Dr. B. Venkateswarly and Dr. S.K. Sharma, Directorate of Rice Research, Rajendranagar, Hyderabad for the facilities extended while doing this research. We are also thankful to Mr. P.V. Ramana Rao, Agronomist and Mr. K. Pundarikakshudu, Farm Incharge, ARI, Rajendranagar who generously permitted to conduct these studies in their farm. Their assistance is gratefully acknowledged. We also extended our thanks to Dr. H. Okajima, Hokkaido University, and Mr. M. Tsuda, Mie University, Japan for their encouragement.

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Fig. 7. Relation between chlorophyll content and mean apparent photosynthesis in Figs. 3 to 6. Symbols ○, ●, △ and × denote cvs. HR59, HR 35, Vijayamahsuri and Sonamahsuri, respectively. Chlorophyll contents of the estimated value computed from the readings of Fuji Green Meter.

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