Photosynthesis of Rice Plant*

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Very few studies which are rather fragmental have been done on photosynthesis of rice plant. At the present time, it is hardly possible to draw a general picture about the effects of environmental factors on photosynthesis of the plant, in spite of the economical importance of the plant in many countries. The authors attempted to elucidate the effect of temperature and light intensity on photosynthesis as well as the diurnal course of its activity of the plant, and the results are reported here.

Methods

The authors devised an apparatus for measuring photosynthetic rate under well-controlled conditions, among which light intensity, temperature, and rate of air flow can be changed accurately and independently. The apparatus consists of seven units to permit six pairs of measurement at a time; in this sort of study dealing with higher plants, reliable comparisons can be made only with the materials sampled at the same time and measured simultaneously under comparable con-

Fig. 1. Apparatus for measuring the photosynthesis of the rice plant.
Only one of the seven units is illustrated.

A: Gas meter	G: Glass spiral	N: Check valve	Wa: Water reservoir
B: Flow meter	H: Phototosynthesis chamber	O: Crank shaft	Na: NaOH reservoir
C: Air-flow regulator	I: Humidity-removing cooler	P: Sintered glass plate	Re: Reflector
D: Moisture supplier	J: Water collector	Q: CO ₂ -absorbing tower	L: Light source
E: Water bath	K: T tube	R: Pipette	Fi: Heat-absorbing filter
F: Thermostat	M: Piston	S: Gas meter	

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ditions, because of the dependency of the photosynthetic activity of the material on the previous history it has undergone.

The construction of single unit is shown diagrammatically in Fig. 1. The air stream forced from an air compressor is divided equally into 14 lines by means of flow-meter (B) and flow-adjuster (C). Each pair of air stream is connected with a pair of photosynthesis chambers (H_1 , H_2) in each unit. In the figure only one line of the air stream is shown for the convenience's sake. Before the air stream is sent to the chamber it is warmed and supplied with moisture by passing through moisture supplier (D). The photosynthesis chamber, 30 cm. high, 3 cm. thick, and 12 cm. wide, is made of wooden frame with removable glass walls on both wide sides. Usually 10 leaves are cut from the plant under water, fixed to the metal net, and placed in each chamber. A small amount of water is contained at the bottom of the chamber, the basal part of the leaves being immersed in it. Then the chamber is placed in the water bath (F) of constant temperature, and illuminated with artificial light (L). A layer of running water 10 cm. thick is served as a heat filter (Fi). Light intensity is adjusted by voltage regulation or the use of appropriate screens in the range up to 100 Klux and is measured by Mazda photometer No. 5.

The air stream derived from the chamber is then cooled in a cooler (I) to be removed of excessive moisture, after which a portion of the air is drawn and forced out by a piston (M) into an absorption tower (Q), containing solution of 1/40 N-NaOH, through a sintered glass plate. The NaOH solution contains 0.1% butyl alcohol as surface-tension depressant. The piston is made of injection tube of 10 cc capacity, and operated by motor power. Check valves (N_1 , N_2) are made of glass tube in each of which a steel ball is enclosed.

At the end of a measurement, the absorbent NaOH solution is transferred into a flask, $BaCl_2$ solution is added, and the residual alkali is titrated with standard 1/20 N- H_2SO_4 , using phenolphthalein as an indicator. Rate of photosynthesis is calculated from the difference in CO_2 content between a measured volume of sampled air derived from the photosynthesis chamber and an equal volume of air sampled at the same time but not having been exposed to the leaf. By similar measurement conducted in the dark, the respiratory rate of the leaf is determined.

After the measurement is finished the leaf area of the sample leaves is determined by contact prints and leaf dry weight, by drying and weighing.

The error of measurement by this apparatus lies within about ± 1 mg./hr./100 cm^2 of leaf area. All the following data are referred to real photosynthesis, unless otherwise noted.

Preliminary Tests

Preliminary tests have shown that the loss of water content from the sample leaves during the measurement period seldom exceeded 11-16 % of the initial water content, causing no recognizable depression in photosynthesis.

The relationship between the rate of air supply and photosynthesis is obtained under the rate up to 100 l./hr./100 cm^2 leaf area, and the authors adopted the rate of 60 l./hr./100 cm^2 , throughout the present study, though the photosynthetic activity at this rate was about 80 % of the maximum value reached at about 100 l./hr./ cm^2 , consuming about 40 % of CO_2 contained in the supplied air.

Well-developed uppermost two leaves were always used, based on the preliminary test showing the effect of aging of the leaf on its photosynthetic activity.

Experimental Results

1. Light Intensity and Photosynthesis

Effect of light intensity on photosynthesis was determined with two varieties, Norin No. 36 and

Rikuu No. 132, at several different growing stages. In the first place, light curve of photosynthesis was determined under 25°C. As given in Fig. 2, the photosynthetic rate increased with the increase in light intensity up to 50-60 Klux, above which it ceased to increase, showing the light saturation. In early growing period, the maximum photosynthetic rate was observed at 50 Klux, thereafter showing a tendency to decline. In later period, however, the light saturation seems to take place at slightly higher light intensity.

Fig. 2 Light curves for photosynthesis of the rice leaves measured at the constant temperature 25 °C

Fig. 3. Light curves for photosynthesis of the rice leaves measured at different temperatures.

As the maximum illumination from direct sunlight and diffused light from the blue sky at noon in summer (at sea level at the latitude of 42° N) is about 106 Klux, the above results suggest that the light saturation occurs at about 50 to 60% of the full sunlight at noon on fine summer days.

Light curves of photosynthesis determined at relatively low temperature (15°C) and high temperature (35°C) are shown in Fig. 3. Because photosynthetic activity varies with the time even in a day and because curves for 15°, 25° and 35°C were deter-

mined with the materials sampled at three different times (7:30, 10:30 and 13:30) of a day, it is apparent that the actual values of photosynthetic rate can not be compared directly among these three curves. However, as the sampling and measurement were made at the same time at any given temperature, the shape of each light-photosynthesis curve is reliable and can, therefore, be compared with each other.

Though the light curves at 15°C are very similar to that at 25°C, the curves at 35°C are quite different from the others, i.e., under high temperatures, maximum rate of photosynthesis takes place at very low light intensity such as 20 Klux, and with higher intensity marked retardation of photosynthesis occurs, especially at later growing periods. These results indicate that the saturating light intensity varies with the temperature, and this variation might be caused by some inhibiting factor.

2. Temperature and Photosynthesis

Photosynthesis in relation to temperature is shown in Fig. 4 and 5. Under sufficient light intensity, no marked difference in photosynthesis was observed over a wide range of temperature from 18.5° to 33.5°C, with only one exception. With the increase in temperature over 39.5°C, however a decrease in photosynthesis is always observed. On the other hand, under low light intensity, quite a different trend in temperature curves was observed; photosynthesis was found to increase with the increase of temperature up to about 38.5°C.

As already mentioned, the light curve of photosynthesis was found to vary with the temperature. Here again the shape of temperature curve also varies with the different light intensity. Thus it was made clear that photosynthesis depends on both light intensity and temperature in such a complicated manner as these two environmental factors exert an interactive effect, as shown schematically in Fig. 6. High temperature and high light intensity seem to interact each other to decrease the photosynthetic rate. It can be suggested from these results that in the southern part of Japan, where the air temperature frequently rises higher than 35°C at midday in summer, there is a high possibility that considerable decrease in the photosynthesis of rice leaf is caused at midday on fine days. There the cool morning and later afternoon or even slightly cloudy days may be

Fig. 4. Temperature curves for photosynthesis of the rice leaves measured under the constant light intensity of 50 Klux.

Fig. 5. Temperature curves for photosynthesis of the rice leaves measured under different intensities of light.

more favorable to the photosynthesis than the hot midday or fine days. On the other hand, in the northern parts where the temperature is relatively low, photosynthesis can go at almost equal rate as that in the southern parts as far as enough light is supplied, and furthermore, the loss of carbohydrates by respiration being less under lower temperature, it can be assumed that the net production rate of dry matter might even be greater than in hot regions. But when once light intensity decreases under rainy or cloudy weather, serious retardation in photosynthesis is inevitable with the accompanying decrease in temperature.

Although the growth of the plant which is also dependent on the temperature is not taken into consideration here, still this discussion might be very contributable to the physiological interpretation of the growth behavior of rice plant under excessively hot weather as well as under cool weather which bears a practical importance in rice production in this country.

3. Diurnal Course of Photosynthesis

(a) Diurnal course of photosynthetic capacity

In order to know the diurnal course of the capacity to carry out photosynthesis, photosynthetic rate was determined under constant temperature and light intensity (28.5°C, 50 Klux) with the sample leaves picked from the plants at different times of the day.

The results obtained on four different days are shown in Fig. 7. On fine days (July 31 and Aug. 21) the diurnal curve, high in the early morning, decreased slightly at midday and increased again in the late afternoon. On cloudy day (Aug. 13), photosynthetic rate was found to be highest

Fig. 6. Photosynthetic activity of the rice leaves in relation to light and temperature.

Fig. 7. Diurnal course of photosynthetic capacity of rice leaf. Sample leaves were taken from the plants at different times of the day and measured at 28.5°C and 50 Klux of light intensity

in the early morning, and continued to decrease throughout the daytime. On Aug. 24, it was heavily cloudy in the morning and less cloudy in the afternoon, and the diurnal curve characteristic to cloudiness observed in the morning was superimposed by the curve associated with the finess in the afternoon.

Based on these results it may be suggested that the observed difference in the diurnal course of

Fig. 8. Diurnal course of photosynthetic capacity. Effect of shading on the capacity. Measured at 28.5°C and 50 Klux.

Fig. 9. Diurnal course of actual photosynthetic rate. Measured at temperature identical to the natural temperature, but under a constant light intensity (50 Klux).

Fig. 10. Diurnal course of actual photosynthetic rate. Measured at temperature and light intensity identical to the natural ones.

photosynthetic capacity is caused by the difference in light intensity to which the leaves have been exposed prior to the measurement. This idea was further supported by the following experiment, in which the effect of artificial shading on the diurnal curve was determined. The test plants were kept shaded since early morning till the time of measurement, and sample leaves were taken at different times of the day and measured of their photosynthetic rate under constant conditions. The curves thus obtained were just the same as the typical curve characteristic to heavily cloudy days, irrespective of the day (Fig. 8)

(b) Actual course or photosynthetic rate in a day

Because the actual course of photosynthetic rate in a given day must be determined not only by the diurnal change of the capacity to carry out photosynthesis but also by the change of light intensity and temperature during a day, measurements were conducted at different times of a day under controlled conditions identical to natural temperature and light intensity. Fig. 9 shows the diurnal curve measured under natural temperature and constant light intensity, and Fig. 10, the actual course of photosynthetic rate measured under conditions identical to the natural temperature and light intensity of a fine day. Here midday depression, sometimes called as "Midday rest of photosynthesis" or "Midday nap", was evidently indicated.

Although various internal and external factors have been investigated and discussed by many workers in connection to the "Midday depression", it still remains unexplained. In the present study there was some resemblance seen between the change of CO_2 content of the atmosphere (Fig. 11) and the curve of photosynthetic capacity. But the midday depression in the actual photosynthesis curve seems to be more reasonably explained by the interaction of high temperature and high light intensity as has been shown in Fig. 6.

Fig. 11. Diurnal change in CO_2 content of atmosphere.

Fig. 12. Relation between temperature and respiratory rate of rice leaf.

From these results it can be concluded that the photosynthesis of rice leaf fully exposed to the sun increases rapidly with sunrise, and after reaching the light saturation it keeps the value with a slight decrease at midday until it begins to decline in the evening. But under hot weather, some midday depression of photosynthesis may take place, especially in southern warm regions.

4. Relationships between Photosynthesis and Respiration

Relating to the influence of temperature on photosynthetic rate of rice leaves, the effect of temperature on respiration was examined at six different temperature levels. The results are shown in Fig. 12, in which the respiratory rate is represented by the output CO_2 mg./gr. dry weight/hr. and expressed in logarithmic scale. Very clear linearity is found between the temperature and respiratory rate. The Q_{10} value calculated from these data was found to give seasonal variation ranging from 1.66 to 2.06 as shown in Fig. 13. At booting stage, the highest value was observed in both the varieties. From these results it can be concluded that the Q_{10} value of respiration in the rice leaf is close to 2, as just it is so with many other kinds of plants, varying somewhat according to the growth stages.

When all the data of photosynthetic rate obtained throughout the whole growing season under a given temperature were plotted against corresponding values of respiratory rate, very clear relationship, almost a linear one, was observed between these two rates at each level of temperature, as shown in Fig. 14, in which both the rates are equally expressed on dry weight basis.

Thus it may be possible to estimate the photosynthetic activity at any growing stage by knowing the value of respiratory rate at that time.

Fig. 13. Seasonal change in Q_{10} value of respiration of rice leaf. The values were calculated from the data obtained within the temperature range from 15° to 45°C

Fig. 14. Relationship between photosynthetic and respiratory rate in rice leaf.

水稻の光合成に関する研究*

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1. 圃場に栽培した水稻農林 36 号及び陸羽 132 号を用い、その光合成作用に及ぼす光及び温度の影響、並びに光合成能力の日変化について研究した。
2. 測定装置には、温度、光及び通気量を自由に且つ独立に変えて、同時に12点の測定を行い得るような通気式の装置を新たに組立てて用いた。測定材料としては、完全に展開した最上位の1, 2番目の葉を用い、その約10枚を切り取って同化室に入れ、60 l/hr/100 cm² 葉面積の割合で外気を通じ、1000 w の電球によつて最大10万ルクスの照明を与えて、30分間に吸収同化されたCO₂量を滴定法によつて定量した。
3. 25°C 及び 15°C の測定では、水稻の葉の光合成作用は4~5万ルクスに於て光飽和に達するが、35°Cではこれよりかなり低い処で最高値を示し、それより強い光の下では反つて抑制される。
4. 5万ルクスの光の下で温度の影響を見ると、広い範囲(18.5°~33.5°C)にわたつて、光合成は殆んど一定の値を示すが、弱光の下では著しく温度に支配され、温度と共に上昇する。
5. このように水稻の葉の光合成は温度及び光の両者の組合せによつてその受ける影響が異り、低温弱光の下で著しく低下するだけでなく、高温強光の下でもかなりの抑制作用を受ける。
6. 水稻の葉の内在的光合成能力はその日の晴曇によつて異つた日変化を示す。即ち晴天の日には朝夕高く日中やや低下するが、曇天の日には朝最も高く午後に至るほど低下する。この現象には前歴としての光の強さが関係することが明かにされた。また盛夏の自然温度、自然照度の下に光合成の日変化を測定すると、いわゆる日中低下現象が見られた。
7. 15°~40°Cの間に於ける水稻の葉の呼吸作用の温度係数(Q₁₀)は時期によつて1.66~2.06の変動を示し、平均1.87であつた。また同一の温度で測定すれば、光合成の強さはほぼ呼吸作用に比例した時期的変化を示す。

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