Photosynthesis of Rice Plant (II)*

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In a previous paper, effect of temperature and light intensity on photosynthesis and diurnal course of photosynthetic activity as well as diurnal course of actual photosynthetic rate of rice plant were reported. The present study was undertaken to determine (1) changes in photosynthetic rate associated with the growth of the plant, (2) varietal difference of photosynthetic rate and (3) effect of CO₂ concentration of atmosphere on photosynthetic rate.

Materials and Methods

Twelve varieties, described below in Table 1, were grown on the paddy field according to the usual culture practices. These varieties are popularly cultivated in this country, and their characters are well known. Four varieties belonging to each group were selected so as to have approximately the same heading time.

From these plants, sample leaves were taken at (1) nursery bed stage, (2) tillering stage, (3) ear-differentiating stage, (4) heading stage and (5) maturing stage. The apparatus and procedures used for measuring photosynthesis were already reported in the previous paper. Conditions given during the measurement were as follows:

1. High temperature (30°C) and high light intensity (40 Klux)
2. High temperature (30°C) and low light intensity (5 Klux)
3. Low temperature (18°C) and high light intensity (40 Klux)
4. Low temperature (18°C) and low light intensity (5 Klux)

Fig. 1. Apparatus for measuring photosynthesis with different concentration of CO₂ of air.
C: CO₂ generator  W: washing bottle  D: distributing bottle  F: flowmeter  A: assimilation chamber

Table 1. Rice varieties used in the study

<table>
<thead>
<tr>
<th>Group of var.</th>
<th>Name of varieties</th>
<th>Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early-maturing</td>
<td>Fujisaka No.5</td>
<td>Resistant to low temperature</td>
</tr>
<tr>
<td></td>
<td>Rikuu No.132</td>
<td>Slightly resistant</td>
</tr>
<tr>
<td></td>
<td>Norin No.1</td>
<td>Intermediate</td>
</tr>
<tr>
<td></td>
<td>Ou No.195</td>
<td>Susceptible</td>
</tr>
<tr>
<td>Medium-maturing</td>
<td>Norin No.25</td>
<td>Preferable to ill-drained paddy, heavy-ear type</td>
</tr>
<tr>
<td></td>
<td>Norin No.29</td>
<td>General use, intermediate type</td>
</tr>
<tr>
<td></td>
<td>Norin No.36</td>
<td>Preferable to well-drained paddy</td>
</tr>
<tr>
<td></td>
<td>Sen-ichi</td>
<td>Native var., much tillering type</td>
</tr>
<tr>
<td>Late-maturing</td>
<td>Norin No.37</td>
<td>Resistant against &quot;Akiuchi&quot;</td>
</tr>
<tr>
<td></td>
<td>Aichi-asahi</td>
<td>Slightly resistant</td>
</tr>
<tr>
<td></td>
<td>Shin-asahi</td>
<td>Susceptible</td>
</tr>
<tr>
<td></td>
<td>Shinriki</td>
<td>Susceptible</td>
</tr>
</tbody>
</table>

At the nursery bed stage the whole tops of twenty seedlings were used for each measurement.

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(1) 30°C, 40 Klux (Sampled at 12~1 pm.)

(2) 30°C, 5 Klux (Sampled at 2~3 pm.)

(3) 18°C, 40 Klux (Sampled at 10~11 am.)

(4) 18°C, 5 Klux (Sampled at 7:30 am.)

Fig. 2. Changes in photosynthetic rate according to growth stage.

and at other later stages about ten pieces of leaf blade taken from the well-developed top leaf and the second leaf on the main stem and the primary tillers were used.

The measurement period was thirty minutes, giving fifteen minutes of pre-illumination. Every determinations were repeated three times at least. Though it took two or three days to complete the determinations of one group, the measurement under a condition of 30°C, 40 Klux was so designed to make it possible to compare not only the photosynthetic rate of four varieties of the group but also all twelve varieties.

Rate of air flow in the photosynthesis chamber was regulated so as the depression of CO₂ content of air not to exceed twenty percent. Generally the estimates of apparent photosynthesis expressed on leaf area basis are shown in the present paper.
The relationship between CO₂ concentration of air and photosynthetic rate was determined by using the apparatus shown in Fig. 1. CO₂ generated in Kipp's apparatus from limestone and hydrochloric acid was fed into the air-stream (normal air or CO₂ free air stream) in the chamber. By this method CO₂ concentration from 1/4 to 4 times of the normal were obtained. In this experiment each leaf as it is attached to the stem was enclosed in the leaf chamber made of plastic, and the outlet air stream was introduced into the measuring apparatus which is specially designed for field use.

The details of the apparatus was already reported. Measuring period was thirty minutes, and the results are expressed again on leaf area basis.

**Experimental Results**

(1) Changes in photosynthetic rate according to growth stage.

From the results illustrated in Fig. 2, the following facts are evidently recognized. Changes in photosynthetic rate associated with growth stage are observed only under high light intensity whatever the temperature is high or low. Photosynthetic rate observed under high light intensity shows its maximum value at the stage when the most active tillering takes place, then the rate decreases until the booting stage and increases again at the heading time. The decrease in photosynthesis after its maximum rate is likely more remarkable with the later maturing varieties than with earlier varieties.

(II) Varietal differences in photosynthetic rate.

By calculating the area enclosed between the photosynthetic rate curve and the abscissa, time axis, of the Fig. 2, we attempted to estimate the relative photosynthetic capacity integrated for the whole growing period of each varieties. In Table 2, the relative values are given, the average of four varies of each group being taken as 100.

By examining the photosynthetic rate curve of each variety and the above values it is apparent, especially with early varieties, that every different variety has a different rate of photosynthesis. However, in this experiment the plants were all grown under the same condition in respect to temperature, light intensity and field conditions, and only during the measurement of photosynthesis the sample leaves were exposed to different temperature and light intensity levels. Consequently the results obtained can not be considered as having direct relation to the varieties described in Table 1. However, the fact that Norin No. 1. showed highest photosynthetic rate under every
condition is likely enough to explain the wide adaptability of this variety, and also the low rates of Ōu No. 195, or the high rate of Rikuu No. 132, under low temp. and low light intensity may be considered as having some relation to their low or high resistance to low temperature.

(III) Photosynthesis and water content of leaves.

As shown in Table 3, very high correlation was observed between photosynthetic rate at different stages of a given variety and water content expressed in percentage of fresh weight of the sample leaves. A negative correlation, though lower than the former but still signi-

![Diagram](image)

Water content (%)

Fig. 3. Correlation between photosynthetic rate at different stages of a given variety and water content of the sample leaves.

× : data at heading time, ○ : data at maturing stage, △ : data at other stages.

Table 4. Correlation between photosynthesis of all varieties at a given stage and water content of the sample leaves.

<table>
<thead>
<tr>
<th>Correlation</th>
<th>Tillering stage</th>
<th>Ear-differentiating stage</th>
<th>Heading stage</th>
<th>Maturing stage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water content</td>
<td>○</td>
<td>○</td>
<td>○</td>
<td>○</td>
</tr>
<tr>
<td>Fresh weight/leaf area</td>
<td>○</td>
<td>○</td>
<td>○</td>
<td>○</td>
</tr>
<tr>
<td>Dry weight/leaf area</td>
<td>○</td>
<td>○</td>
<td>○</td>
<td>○</td>
</tr>
<tr>
<td>Water/leaf area</td>
<td>○</td>
<td>○</td>
<td>○</td>
<td>○</td>
</tr>
</tbody>
</table>

Abbreviations same as Table 3.

significant at 5% level was found between photosynthetic rates and dry weight per unit area of leaves. It can, however, be accounted for by the fact that the dry weight per unit leaf area has a close, negative cor-
relation with the water content of the leaves. The fact that photosynthesis has certain correlation with water content of leaves, but not with the amount of water per unit leaf area suggests that the effective factor is the concentration itself, and not the actual amount of water in the tissue.

In Fig. 3, examples of correlation between photosynthesis and water content of leaf are shown. It is interesting that the photosynthetic rates at the stage from heading time to early maturity are always located above the regression line. Thus the photosynthetic values observed at that stage are greater than the values expected on the basis of water content, showing some other factor or factors are effecting the photosynthetic activity at that stage.

Similar interpretation of the photosynthetic rates of all varieties observed at a given stage of growth resulted again in a high correlation between photosynthetic rate and water content (Table 4, and Fig 4) with the exception of that at the tillering stage.

IV. Temperature coefficient of photosynthesis.

Table 5. Q10 value of photosynthesis (40 Klux, 18~30°C)

<table>
<thead>
<tr>
<th>Group</th>
<th>Apparent photosynthesis</th>
<th>True photosynthesis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early</td>
<td>1.01</td>
<td>1.09</td>
</tr>
<tr>
<td>Medium</td>
<td>1.05</td>
<td>1.12</td>
</tr>
<tr>
<td>Late</td>
<td>1.03</td>
<td>1.07</td>
</tr>
<tr>
<td>average</td>
<td>1.03</td>
<td>1.09</td>
</tr>
</tbody>
</table>

* Average of twenty determinations; average value of four varieties determined at five different stages.

Fig. 5. Temperature coefficient of true photosynthesis. Obtained under 40 Klux light intensity and two levels of temperature, 18°C and 30°C. Each line represents average of four varieties.

Fig. 6. Effect of long time exposure of leaf to high concentration of CO₂ on its photosynthetic activity (CO₂ mg/hr/100 cm²). Senbon-asahi, pot culture. 16 Aug. Average of duplicated measurements.

Temperature coefficient of photosynthesis was calculated with the data obtained under 40 Klux

Fig. 7. Photosynthetic rate of rice leaf in relation to the concentration of CO₂ of air.
light intensity and two levels of temperature, 18°C and 30°C. In Table 5 the average value of Q10 of each three groups of varieties are shown. Figures in the table indicate the average Q10 of the four varieties determined at five growing stages. The seasonal phase of Q10 value of true photosynthesis is illustrated in Fig. 5. That temperature has almost no effect on photosynthesis carried on under high light intensity and normal CO2 concentration of air was already described in the previous paper. The results of the present paper proves clearly that this relationship still exists with different varieties over the whole growing period.

(V) CO2 concentration and photosynthesis.

Using the apparatus described above the photosynthetic rate of intact rice leaf in relation to CO2 concentration of air was studied. In this experiment the leaf as it is attached to the plant growing in paddy field or in pot was used. The direction of leaf surface was kept unchanged from natural condition during measurement, and light intensity at the surface of the leaf was measured. A preliminary test was undertaken to examine the effect of long time exposure of leaf to high concentration of CO2 on its photosynthetic activity. The leaf exposed to the four times normal CO2 concentration for about six hours showed higher rates of photosynthesis than the leaf exposed to normal concentration during the exposure (Fig 6). Increase of photosynthesis was 15-63%, showing large variation, but any sign of toxic effect of high CO2 concentration was not observed during this period.

Then, photosynthetic rates with half normal, normal, twice normal, three times normal and four times normal CO2 concentration were measured, and the results are shown in Fig. 7. It is apparent that photosynthetic rate of rice leaf increases with increasing CO2 concentration up to about twice normal concentration under the natural condition of fine day. With the half normal CO2 concentration the outlet air was still found containing more than 0.014% CO2. This indicates that the decreased photosynthesis with half normal CO2 concentration is not directly caused by the exhaustion of supplied CO2.

In connection with this experiment the fluctuation of CO2 content of normal air on rice field was examined. As reported in the previous paper, variation ranging 0.50-0.60mg. CO2/l was observed. Within this range of variation increment of 0.1mg. CO2/l gives an increase of about 2mg CO2 absorbed/hr./100cm² of leaf area. As the photosynthetic value under fine day is approximately 20mg. CO2/hr./100cm², the change of photosynthetic rate caused by fluctuation of CO2 content of air may be concluded as being about 10 percent at the greatest. On the other hand, the possibility of increasing photosynthetic rate by supplying CO2 into air of rice field by some means is suggested.

摘 要
水稻の光合成に関する研究（第2報）

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光合成は光の強さ、温度、大気中のCO2濃度などの環境条件によって左右されると共に植物体の内在的要因によっても支配される。光及び温度との関係は既に前報で報告したところであるが、本報では更に外的要因としての大気中のCO2濃度、外的要因に関しては生産に伴う光合成能力の変動、光合成の品種間差異を研究し、それらの変化が植物体のいかなる生理的状態と関係しているかを明らかにせんとした。

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実験材料と方法

早中、晩生に属する代表的水稻品種で出穂期のほぼ等しいものを4品種つつの選び（第1表）これを圃場圃場に栽培し、前期に述べた測定方法によって苗期、分け期、幼穂分化期、出穂期及び成熟期の5回に亘って次の5種の測定条件の下で光合成の強さを測定した。

測定条件: (1) 高温 (30℃), 強光 (40 Klux) (3) 低温 (18℃), 強光 (40 Klux), (2) 弱光 (5 Klux) (4) 弱光 (5 Klux)

大気中 CO₂濃度と光合成との関係を研究するには第1回の装置を用い、ポット苗は圃場に生育する水稻の葉を1枚つつの収穫した後の架橋に入れる。大気中 CO₂濃度の1/2から4倍の濃度の CO₂を含む空気を送って光合成を測定した。その測定装置は別に発表した圃場用移動式光合成測定装置による。

実験結果

（1）生育に伴う光合成能力の変化。第2回に示す如く、生育に伴う光合成能力の変化は品種とも強光の下でのみ認められ、弱光の下ではほとんど時期別差異が見られない。これは温度にかかわらず成り立つ。強光下で見られる光合成能力は何れの品種も分け期時稲本田での最高を示し、以後低下し、出穂期には再び高まる、生育前期の低下は晚生種ほど著しい。

（2）光合成能力の品種間差異。4種の条件下で測定された各品種の光合成能力を比較するため、光合成曲線と水平軸でかかれた面積を求め、早、中、晩グループ内の平均値を100として表示すれば第2表の如く、特に早生で明かに品種間差異があり、農林1号はすべての条件でその値が高く、陸羽132号は高温では特に高く、低温弱光下では最も高く、奥羽195号は常に低く、これらの結果は農林1号の広い適応性とか、陸羽132号の耐冷性や弱という特性と関係があるものと考えられる。

（3）光合成の強さと葉内水分含量。同一品種につき各生育時期の光合成の強さと葉内水分％とは高い相関（第3表及び第3回）がある。また葉面積当たり乾物重も有意な相関があるが、乾物重/葉面積が葉内水分％と高い相関があるためである、水分率/葉面積との間には相関がないから光合成に影響するのは水の絶対量ではなくて、組織内濃度であることが示される。偏出穂から成熟初期の光合成は水分％から予期される以上の光合成を行っており、水分以外の要素が原因しているらしい。また同一生育時期の各品種の光合成についても同様に葉内水分％（新鮮重に対する％で表示）との相関がある（第4表及び第4回）。

（4）光合成の温度係数。多数の品種につき全生育期間に亘り光合成のQ₁₀値は1に近いことが示された。

（5）光合成と大気 CO₂濃度。普通の濃度の4倍の CO₂濃度を含む空気中で6時間光合成を行わせたが光合成は15～63％の増加を示し、別に害作用は認められなかった（第6図）。そこで普通の濃度の1/2から4倍の濃度の CO₂を含む空気を通じて光合成を測定すると第7図の如く、普通濃度の2倍では濃度の増加と共に光合成は増加する。圃場に於ける大気の CO₂含有率は0.50～0.60mg/lの範囲であるが、この範囲では CO₂の0.1mg/lの変化に対して光合成の増減はおよそ2mg CO₂/hr./100cm²であり、他方普通晴天日の水稻の光合成は20mg CO₂/hr./100cm²内外であるから、CO₂含有の変動による光合成の変動は10％程度である。このことは第9図の結果と共に、大気中の CO₂濃度を増加せしめることによって光合成を促進せしめ得ることを示唆している。