Efficiencies of Solar Energy Conversion in Rice Varieties
as Affected by Planting Density*

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The pronounced importance of light as a factor determining the dry matter production of chlorophyllous plants reveals a possibility to increase crop yield by a better use of solar energy. The efficiency of solar energy conversion of crop plant is usually calculated as a percentage of chemical energy of dry matter produced in plant in a period to the corresponding incident solar energy at the top of the plant. The advantage of calculating the real efficiency of dry matter production including respiratory loss is obvious for physiological studies, but the estimation of such real efficiency tends to be erroneous when the corresponding respiratory study is not available. What matters when the growth of crop plant as a whole is being considered is the net daily contribution of photosynthesize to the accumulation of dry matter in plant and in this sense the apparent efficiency would be of more interest.

The apparent efficiency can further be divided into two parts; the efficiency of intercepting solar energy and that of dry matter production utilizing the intercepted energy. The whole aspect of these efficiencies which ultimately determines the total dry matter production is obtainable if the intercepted energy as well as incident energy is continuously measured over a whole growing season. Despite its high efficiency in producing carbohydrates compounds for human food little is done to analyse the growth and yield of rice plant in relation to the above efficiencies.

The objects of the experiment described in this paper is first, to know how these efficiencies of rice crop vary with growth, variety and planting density, and, second, to examine whether there is any relation between the pattern of change in the efficiencies and the partition of total dry matter to the grain yield.

MATERIALS AND METHODS

Five varieties, Kusabue, Norin 22, Norin 29, Norin 8 and Kinmaze, almost similar in heading period but different in growth habits, were sown in nursery bed on 7 May, 1965. The seedlings of nearly 6th leaf stage were transplanted to paddy field on 17 June, with a rate of two seedlings per hill, into three different densities; 24 cm x 36 cm, 24 cm x 24 cm, 24 cm x 12 cm. The treatments were arranged in split plot design and replicated in three blocks. To assure good growth, a relatively heavy basal dressing was applied and top dressing was repeated twice before heading.

The plots were sampled on six occasions; 17 June (t1), 19 July (t2), 6 Aug. (t3), 27 Aug. (t4), 16 Sep. (t5) and 13 Oct. (t6). On each occasion a sample consisted of the crop in 0.7 m² of land was taken from random position in the plot. The crop in a sampled area was cut at ground surface due to the difficulty to recover the whole roots. The whole sample was weighed, a 100 g sub-sample before heading and 300g after heading was taken, dried at 100°C, weighed, and the total dry weight of whole sample was calculated by the usual method. The remainder of the sample was used for rating to estimate the leaf area index (LAI). The general procedure of rating was followed to the method by Waston et al., but a little modification for rice plant by Hayashi was added. In particular, the area of leaf sheath was omitted due to its negligibly small photosynthesis in rice plant, and the number of shoots rated per a sample was increased.

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to 50 to get a better estimate of LAI.

Solar energy was measured by six tube-type radiometers with a sensitive range between 0.3 and 4.0 μ, one was placed in open as a control and the other were separately placed in each plot of the same density. Each radiometer, 3 cm in diameter and 40 cm in length, was inserted in the middle of 24 cm apart rows in pararell to them just above the water surface, and was so placed that the extent of shade was averaged over the entire length of sensitive part of radiometer. Light transmission of three different densities were equally measured by moving the five radiometers as one set in every four days from thin to medium, medium to dense and dense to thin again. All radiometers were connected to a automatic recorder and by running the recorder over the whole growing season the time trend of solar energy at the top and bottom of crop of every plot in block II was obtained. Those for block I and III were estimated by using the LAI of each plot and the LAI-percent transmission curves of corresponding plots in block II, assuming that the curves were commonly applicable for three blocks.

The efficiency of intercepting solar energy (Ei) and that of utilizing the intercepted energy for dry matter production (Eu) were calculated as follows:

$$Ei(\%) = \frac{\text{absorbed energy} + \text{reflected energy}}{\text{total incident energy}}$$

$$= \frac{\text{total incident energy} - \text{transmitted energy}}{\text{total incident energy}}$$

$$= 100 - \text{(percent transmission)}$$

$$Eu(\%) = \frac{\text{fixed energy}}{\text{intercepted energy}}$$

$$= \frac{4000 \times \text{fixed dry weight}}{\text{total incident energy} \times Ei} \times 100$$

* 1 gram dry weight was assumed equivalent to 4000 cal.

**RESULTS**

The seasonal change in the incident energy showed considerable decrease three times during the growing season (fig. 1). The first decrease was due to a prolonged rainy season, the second one just before heading was an exceptionally bad weather and the third one in ripening period

<table>
<thead>
<tr>
<th>Table 1. Changes with time and planting density in the efficiency of intercepting energy (Ei), utilising energy (Eu) and converting energy (Ec), of Kusabue (Ku), Norin 22(N22), Norin 29(N28), Norin 8(N8) and Kinmaze (Kin).</th>
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<td>Thin planting</td>
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was a typical example which had long been pointed out as a factor limiting the rice production in this part of Japan. The average over the whole growing season was 346 cal \cdot cm^{-2} \cdot day^{-1} and for about one month before heading was the only main period surpassed the average. Consequently, the growth of rice crop was generally not vigorous and even the highest LAI at heading was still below 6 ranging 2.7 for Norin 22 in thin plot to 5.8 for Kinmaze in dense plot.

The amount of dry matter production (W) was expressed in the following form by using the two efficiencies presented in foregoing paragraph

\[ W = I \times E_i \times E_u \]

where I was the incident solar energy. Changes in Ei and Eu was shown together with the efficiency of solar energy conversion (Ec) which was the product of Ei and Eu (table 1). Ei was very low in first one month, increased rapidly towards heading, and after heading there was a little further increase before attaining the maximum which lasted almost plateau till haevest. Ei also simply increased with increase in density, but a marked difference between densities in earlier period lessened as the growth advanced.

Table 2. Correlation coefficients between the dry weight increase (\(dW\)) and the efficiency of intercepting energy (Ei) and that of utilizing energy (Eu).

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<tr>
<th>( \text{at} )</th>
<th>( t_1 )</th>
<th>( t_2 )</th>
<th>( t_3 )</th>
<th>( t_4 )</th>
<th>( t_5 )</th>
<th>( t_6 )</th>
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<tr>
<td>( dW : E_i )</td>
<td>.946**</td>
<td>.888**</td>
<td>.321</td>
<td>.426</td>
<td>.288</td>
<td></td>
</tr>
<tr>
<td>( dW : E_u )</td>
<td>.805**</td>
<td>.474</td>
<td>.558**</td>
<td>.983**</td>
<td>.959**</td>
<td></td>
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</table>

Note:** significant at 1 % level.

Eu, on the contrary, changed rather variously and any clear relation was not detected except in some plots it reached to maximum at booting stage \((t_1 - t_2)\). Ec, therefore, increased with the advance in growth till heading, after then followed in most cases a gradual decrease. Generally, Ec showed a convex curve over the whole growing season with a maximum of about 2 %, but in some plots a slight increase occurred in latter part of ripening.

To know which efficiency was the first determinant of \(dW\), increase in dry weight in each growing period, the correlation coefficients between \(dW\) and both efficiencies (Ei and Eu) were separately calculated (table 2). Only in earlier stage of growth Ei correlated almost linearly with \(dW\), but from booting stage afterwards the correlation between \(dW\) and Eu dominated, particularly after heading their relation was completely linear. A high correlation between \(dW\) and Eu in the earliest period was attributable to a marked high correlation found only in dense plot when the leaf area and hence \(dW\) in other plots was confined in a smaller range.

Summing up the total energy of incident, intercepted and utilized the overall relation for the whole growing season was demonstrated (fig. 2). Both Ei and Eu increased with increase in density from thin to medium for all varieties, but a further increase in density caused a decrease in Eu for Norin 22, Norin 29 and Norin 8. Only Kinmaze and Kusabue maintained the increase both in Ei and Eu even in dense plots. As a consequence, all varieties increased dry matter production significantly with increase in density from thin to medium. From medium to dense, however, similar increase was followed by only Kinmaze and Kusabue, and the rest varieties stayed at the

Table 3. Correlation coefficients between the efficiency of utilizing energy (Eu) and photosynthetic efficiency (\(dW/D\)).

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<th>( \text{at} )</th>
<th>( t_1 )</th>
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<tr>
<td>Eu : (dW/D)</td>
<td>.288</td>
<td>.292</td>
<td>.723**</td>
<td>.862**</td>
<td>.893**</td>
<td></td>
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Note:** significant at 1 % level.
same level of dry matter production because the increase in Ei was offset by the decrease in Eu. Including all plots Ei ranged from 45 to 66%, Eu from 1.5 to 2.1% and Ec from 0.7 to 1.4% which corresponded to 714 to 1,429g of dry matter production per square meter of land. It was also noticed that Norin 22 with a relatively low Ei and high Eu performed an efficient dry matter production which eventually attained to nearly a same level with other varieties.

Above results clearly demonstrated the importance of Eu, since the changes in Eu remarkably reflected on the changes in dry matter production. Eu was the efficiency of utilizing the intercepted energy for dry matter production, so was expected to correlate with the efficiency of photosynthesis of crop community. This was examined by calculating the correlation coefficient between Eu and \( JW/D \), which is the ratio of dry weight increase (\( JW \)) to leaf area duration (D) and is conveniently used as a simple expression of an averaged efficiency of apparent photosynthesis (table 3). The correlation coefficients, very low in earlier growth though, consistently increased till harvest, and in ripening period their relation became nearly linear. This and foregoing results
made clear the role of Eu for $\Delta W$, i.e. Eu determined $\Delta W$ through the efficiency of photosynthesis expressed as $\Delta W/D$.

To convert the total dry weight at harvest to grain yield one more efficiency usually called as harvest index$^{13}$ should be considered. Substituting yield by ear dry weight the partitioning of dry matter of matured crop was examined (fig. 3). Harvest index of Norin 29 and Norin 22 was almost unchanged for the experimental range of density, whereas that of Kinmaze, Kusabue and Norin 8 decreased as the density increased. The former varieties had an obvious advantage of almost unchanged harvest index with which they gave a relatively stable yield for a given amount of total dry matter production. The latter varieties were, in this sense, less efficient since they should produce a far enough dry matter to compensate the decrease in harvest index to get a higher yield. Still, Kinmaze yielded highest among the varieties tested and also in many other experiments not described here, and the advantage of this sort of variety will be discussed later.

For an easier comparison of varietal performance in this experiment all changes in the efficiencies were shown in relation to the changes in dry matter production and yield (fig. 4). Norin 29 and Norin 22 behaved similarly marking one group, Kinmaze and Kusabue another group. Norin 8, the oldest variety of all, failed to follow the changes in the efficiencies of any group and showed little possibility to get a higher yield.

**Discussion**

The efficiencies of solar energy conversion (Ec) in this experiment were somewhat lower than those reported by other workers. Kamel$^{19}$ reported 2.9% for barley and 4.4% for mangold as the average efficiency during the entire growing season, but those efficiencies were calculated with visible radiation basis, i.e. photosynthetically effective radiation, which was assumed as 45% of total incident radiation. Assuming that the visible radiation was 47% of total incident radiation Yocum et al.$^{17}$ reported the efficiency of dense corn crop as high as 5.1% for the momental measurement around noon and 3.2% for the average of whole day. If similar assumption, visible is 47% of total, is applied to the above results the assumed efficiencies of solar energy conversion for the rice varieties range from 2.5 to 4.4% as the maximum at booting stage and 1.4 to 3.0% as the average over the whole growing season. Had the root weight included they would have even been higher.

Strictly, a simple subtraction of transmitted energy from total incident energy does not give the real energy effective for photosynthesis, since as was shown by Yocum et al.$^{17}$ the transmitted energy is rich in green region which is less effective for photosynthesis. The albedo loss (reflected light) which is included in Ec also remains as another uncertainty.

The reversal from Ei to Eu for the first determinant of $\Delta W$ at middle stage of growth manifested a notable feature of light utilization in crop community (table 2). In earlier stage of growth when the mutual shading of leaves was not severe $\Delta W$ was directly increased by the increase in intercepted energy, suggesting that all leaves responded with their maximum capacity of photosynthesis. In middle stage when LAI was about maximal the heavy mutual shading lowered the photosynthetic rate of leaves inside the crop. Consequently, $\Delta W$ related more to Eu, the efficiency of utilizing the intercepted energy available for photosynthesis, than to Ei, the efficiency of intercepting the incident energy.

In later stage all leaves particularly upper leaves tend to be more horizontal and the light transmission of crop is worsened relative to its LAI$^{15}$ and the emerged ears also intercept the incident light. Thus the decrease in LAI was offset by the worsened arrangement of leaves and the emerged ears, resulting in an unchanged or even worsened deficiency of light inside the crop. This was reflected in a very close linear relation between $\Delta W$ and Eu (table 2), and also in Ei which lasted almost plateau after heading despite the
decrease in LAI (table 1).

Norin 29 and Kinmaze yielded almost equally, but they made a clear contrast in the response to the increase in density. For Norin 29, Eu increased with increase in density from thin to medium but it decreased considerably with further increase in density, suggesting a less possibility of a further increase in dry matter production (fig. 2). But the almost unchanged high harvest index enabled this variety to attain a higher yield relative to its total dry weight (fig. 3). For Kinmaze, on the contrary, harvest index decreased with increase in density, suggesting a necessity of bigger dry matter production for a higher yield (fig. 3). Eu of Kinmaze consistently increased with increase in density (fig. 2) and this certainly compensated well enough the decrease in harvest index (fig. 3). Hayashi et al. reported a higher crop growth rate of rice varieties by a smaller extinction coefficient of light which correlated to a more erect habit of leaves. So, it was most likely that the advantage of Eu in Kinmaze was due to its better arrangement of leaves, since the upper leaves of this variety were maintained nearly erect even in the ripening period. Further studies will be needed to know what characteristic is responsible for the response of Norin 29-type and of Kinmaze-type.

SUMMARY

In earlier stage of growth dry matter production of rice varieties growing in the field was determined mainly by the efficiency of intercepting incident energy (Ei), whereas in middle and later stage it was determined mainly by the efficiency of utilizing the intercepted energy (Eu).

The average efficiency over the whole growing season ranged from 45 to 66 % for Ei, 1.5 to 2.1 % for Eu, and the corresponding efficiency of converting the total incident energy to dry matter (Ec), the product of Ei and Eu, ranged from 0.7 to 1.4%. For obtaining a higher yield, two different types of response to the increase in planting density were distinguished among the varieties tested. One were those which compensated the decrease in Eu by a relatively stable harvest index (Norin 29-type) and the other compensated the decrease in harvest index by a consistent increase in Eu (Kinmaze-type).

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LITERATURE CITED

水稲品種の光利用効率と栽培密度との関係

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光利用効率を、群落が光をまず受けとめる効率 (Ei) と、受けとめた光を利用して光合成により乾物として固定する効率 (Eu) とに分解すると、乾物生産量 = 役下エネルギー × Ei × Eu という関係が成り立つ。水稲中生5品種を、粗・中・密の栽培密度で圃場栽培し、一方、群落内外の光の強さを連続測定して、これらの効率と乾物生産、収量との関係をしらべて次の結果を得た。

1) 繊細度の低い生育前期の乾物生産は主として Ei により、繊細度の高い中後期は主として Eu により決され、特に出穂後の乾物生産と Eu とは密接な直線的関係を示した。
2) 全生育期間の平均 Ei は 45～66％、平均 Eu は 1.5～2.1％、役下全エネルギーに対する乾物生産平均効率 (Ec=Ei×Eu) は 0.7～1.4％ であった。
3) 栽培密度増加とともに Ei, Eu も相まって上昇すれば乾物生産も増加したが、Ei の上昇が Eu の下降によって相殺されると、乾物生産も増加しなかった。
4) Eu は生育後半期の（乾物増加率）/（収穫係数）と密接な直線的関係を示し、Eu が群落の光合成能率により規定されることを示唆した。
5) 収量 = 乾物重×収穫指数（harvest index）とすると、栽培密度増加による収穫指数の低下程度には品種間差異があった。
6) 栽培密度増加とともに、Eu が低下して大形な乾物生産増加の可能性は低いが、収穫指数が比較的安定しているために多収の農林29号型と、Eu がさらに増加して乾物生産が大形に増加し、収穫指数の低下を補うために多収の金南風型との、二つの型を類別できた。