Japan. Jour. Crop Sci. 50(2) : 223-232 (1981)

Dependence of Potential Productivity and Efficiency for Solar Energy Utilization on Leaf Photosynthetic Capacity in Crop Species

Yoshio MURATA
(*Faculty of Agriculture, the University of Tokyo, Bunkyo-ku, Tokyo 113*)
Received October 31, 1980

There are controversial discussions on the comparison of potential productivity of C_3 and C_4 species. In relation to the results of the IBP carried out in 1960s, LOOMIS and GERAKIS[14] collected high values in the net production per unit land area in a season, Pn, in various crop species cultivated under very favorable field conditions at different locations in the world. They examined the data and classified them in terms of latitude, arriving as a result at the following hypothesis: In the tropical and subtropical regions, C_4 species show far higher productivity than C_3 species, in temperate regions the difference between the two groups decreases, and in cool temperate regions C_3 species attain superiority.

Part of this result was explained by MONTEITH[15] with the difference in the length of growing season. Therefore, it is obvious that species comparison must be made under the condition free from the influence of growing days. For this purpose, either the mean crop growth rate (mean CGR) or the maximum crop growth rate (maxCGR) can be used. The former is calculated by dividing the Pn value with the length of growing season, and the latter is obtained by observing the highest short-term CGR value during the whole growth duration of a species.

In relation to these problems, GIFFORD[6] reported, by use of various published data on productivity as well as biochemical and physiological ones, that, although C_4 species show considerably higher efficiency in their photosynthetic mechanism as compared with C_3 species, their superiority decreases at the leaf tissue level, and even becomes equal at the maxCGR level.

However, COOPER and TAINTON[2] and COOPER[3] compared the values of maxCGR of grass species cultivated under favorable field conditions, obtaining an average value of 30.3 g/m^2/day for the C_4 species and that of 19.5 g/m^2/day for the C_3 species. KAWANABE[9] compared the relative growth rate, RGR, of 15 grass species under various temperatures in a phytotron and obtained the highest RGR value of 15% per day for the C_3 species under the optimum condition of 27°C/22°C in day/night temperature, whereas the highest RGR for the C_4 species was nearly twice the former value, obtained at the higher, optimum temperature of 36°C/31°C. Further, MONTEITH[15] reexamined the maxCGR data quoted by GIFFORD[6] and came to the conclusion that the reliable data so far available suggest the superiority of the C_4 species to the C_3 species.

In these discussions, the productivity values have never been compared among species in relation to the photosynthetic ability of the leaf, p_0, which represents the highest value in apparent photosynthetic rate of each species under natural conditions. It is well-known that p_0 differs considerably not only between C_3 and C_4 groups, but also among species within a group as well as among varieties of the same species. However, little evidence has so far been obtained which demonstrates the effect of p_0 on the biological or economic yield of crop species. In the case of economic yield, not only p_0, LAI and canopy structure, but also "sink" capacity, translocation ability and other factors are involved in the yield-formation process, so that it will be no wonder if p_0 cannot be

Table 1. Comparison among various crop species of high values in maxCGR, efficiency for solar energy utilization, Eu, and maximum leaf photosynthetic activity under natural conditions, p_0

Species	CO_2fix pathway	Location	maxCGR $g/m^2/day$	Solar rad. ly/day	Eu %	p_0 $mgCO_2/dm^2/hr$
Nepiergrass	C_4	Puerto Rico[5]	60	—	—	84 a
Corn	C_4	Fukuoka, Japan[24]	55	485	4.6	60 b
〃	〃	Shiojiri, Japan[18]	52	486	4.3	
〃	〃	Calif.[13]	52	736	2.9	
〃	〃	New York State[13]	52	500	4.2	
Rice, *indica*	C_3	Philippines[25]	55	564	3.7	48 c
〃, *japonica*	C_3	Chikugo, Japan[18]	36	478	2.8	36 d
〃, *ind.* x *jap.*	C_3	Takada, Japan[22]	35	487	2.7	35 [23]
Pearl millet	C_4	N.T. Australia[18]	54	510	4.2	60 e
Cattail	C_3	Calif.[5]	53	—	—	55 f
Sorghum	C_4	Calif.[13]	51	690	2.9	51 g
Sugarcane	C_4	Hawaii[7]	44	—	—	52 h
Oats	C_3	Kitamoto, Japan[23]	40	338	4.7	28 [23]
Barley	C_3	Kitamoto, Japan[23]	38	338	4.5	25 [23]
Potato	C_3	Calif.[5]	37	—	—	26 i
Sunflower	C_3	Tokyo, Japan[27]	37	—	—	33 [27]
Italian ryegrass	C_3	Tochigi, Japan[20]	35	439	3.2	18 j
Sugarbeet	C_3	U.K.[13]	31	294	4.1	28 k
〃	〃	Sapporo, Japan[18]	28	413	2.8	30 l
Wheat	C_3	Kitamoto, Japan[23]	30	338	3.6	27 [23]
Soybean	C_3	Morioka, Japan[18]	27	290	3.6	27 m
Sweet potato	C_3	Kagoshima, Japan[10]	21	—	—	21 n
Groundnut	C_3	Nigeria[21]	21	—	—	27 o
Orchardgrass	C_3	U.K.[13]	19	331	2.8	22 p

Data source for p_0: (common to Tables 1 and 2) a Ludlaw & Wilson, b Heichel & Musgrave, 1969, 25-80 mg; c IRRI, 1968, 34-62 mg; d Ishihara et al., 1977, and others, 31-42 mg; e Muramoto et al, 1965; f McNaughton & Fullem, 1970, 44-69 mg; g Stephensen et al, 1976, and others, 42-60 mg; h Irvine, 1968, 34-86 mg; i Chapman & Loomis, 1953; j Murata & Iyama, 1963; k Hofstra & Hesketh, 1969, and others, 24-30 mg; l Oshima, 1962; m Ojima & Kawashima, 1968, 22-31 mg; n Tsuno & Fujise, 1965, 19-24; o Bhagsari & Brown, 1976, 24-37 mg; p Hesketh, 1963, and others, 13-31 mg; q Mahon et al, 1977, and others, 17-28 mg; r Corley et al, 1973; s Samsuddin & Impens, 1979; t Murata et al., 1965; u Dornhoff & Shibles, 1965, and others, 18-43 mg; v Pallas, 1973, and others.

directly correlated with economic yield as with the cases in many reports. However, in the case of maxCGR, the situation seems to be rather simple, with only the three major plant components, i.e., p_0, LAI, and canopy structure, needed to be considered.

The present author, therefore, has examined the possible relationships, among various crop species, of p_0 with maxCGR as well as mean CGR collected from various reports. In addition, the solar energy utilization efficiency corresponding to each maxCGR value was compared among species.

Materials and Methods

High values of maxCGR for various crop species were collected from literature, together with the amount of incident solar radiation during the period for the max-

CGR determination (Table 1). High Pn values were also collected together with the length of growing season to calculate the mean CGR values (Table 2).

In selecting the p_0 value for a species, priority was given to those p_0 values which were obtained with the same or similar material as used for the productivity determination. Otherwise, the average of the reported values for the species in question was adopted.

The solar energy utilization efficiency, Eu, was expressed by the ratio of the total combustion energy contained in the dry matter, ΔW, produced on a unit field area during a definite period to the total short-wave solar radiation, S, incident on the plants during the same period, as shown by the following equation:

$$Eu=\frac{H\cdot \Delta W}{S}\times 100\% \qquad (1)$$

where H stands for heat of combustion per gram of dry matter. However, Eu is not necessarily expected to change in reverse proportion to S, because ΔW will change at the same time. In order to know the true relationship between Eu and S, analysis was made with the data of the Maximal Growth Rate Experiments of IBP carried out in Japan by the Local Productivity Group[18].

Results and Discussions

1) *Relationships of p_0 with maxCGR and mean CGR*

The relationships between p_0 and max-CGR are shown in Fig. 1. Here, a correlation coefficient as high as 0.778 is found for the C_3 species, and 0.826 for the C_4 species. When the two groups are mixed, the linear correlation becomes as high as 0.886.

Table 2. Comparison among various crop species of high values in the net production per year (Pn), growing days, mean crop growth rate (mean CGR), and leaf photosynthetic activity (p_0)

Species	CO_2-fix pathway	Location	Pn t/ha/year	Growing days	mean CGR $g/m^2/day$	p_0, mg $CO_2/dm^2/hr$
Nepiergrass	C_4	Puerto Rico[14]	85.9	365	23.5	84 a
Sugarcane	C_4	Hawaii[14]	67.3	365	18.4	52 h
Sorghum	C_4	Calif.[14]	46.6	210	22.2	51 g
Sugarbeet	C_3	Calif.[14]	42.4	290	14.6	28 k
〃	〃	Sapporo, Japan[18]	22.9	175	13.1	30 l
Cassava	C_3	Java[14]	41.0	365	11.2	26 q
New sorgo	C_4	Gifu, Japan[19]	40.3	142	28.4	—
Oil palm	C_3	Malaysia[4]	40.0	365	11.0	20 r
Bermudagrass	C_4	Puerto Rico[14]	37.3	365	10.2	39 j
Rubber	C_3	Malaysia[4]	36.0	365	9.9	20 s
Corn	C_4	Italy[4]	34.0	140	24.3	60 b
〃	〃	Shiojiri, Japan[18]	26.5	128	20.7	
Alfalfa	C_3	Calif.[14]	29.7	250	14.1	26 t
Rice, *indica*	C_3	Philippines[25]	20.0	125	16.0	48 c
〃, *japonica*	C_3	Fukui, Japan[18]	19.7	161	12.2	36 d
Potato	C_3	Calif.[14]	22.0	129	17.0	26 i
Pearl millet	C_4	A.C.T. Australia[1]	21.7	117	18.5	60 e
Sweet potato	C_3	Kagoshima, Japan[10]	20.5	169	12.1	21 n
Oats	C_3	Kitamoto, Japan[23]	18.5	243	7.6	28 [23]
Barley	C_3	Kitamoto, Japan[23]	15.3	203	7.5	25 [23]
Soybean	C_3	Iowa[14]	10.4	110	9.5	31 u
〃	〃	Morioka, Japan[18]	9.4	113	8.3	27 m
Groundnut	C_3	Tanzania[21]	15.5	125	12.4	27 v

Although direct evidence is needed, this figure may be interpreted as suggesting that the maxCGR is most heavily dependent on the leaf photosynthetic ability, as far as the species difference is concerned, regardless of the C_3 and C_4 discrimination. In addition, it is suggested that, in the C_3 species which have generally lower p_0, the effect of its increase to promote productivity is larger than in the C_4 species which have higher p_0. Because, it is calculated that the linear regression coefficient of maxCGR on p_0 is 0.824 for the C_3 species against 0.366 for the C_4 species. Thus, a second order regression seems to fit for covering all the C_3 and C_4 data. The correlation coefficient between the observed values and those calculated by the second order equation shown in Fig. 1 was 0.896.

Under the conditions where high values of maxCGR were obtained, such environmental factors as light intensity, temperature, and supply of water and nutrients may be considered to have been nearly at their optimum levels, with their LAI attaining the maximum values, and consequently, minimizing its effect on dry matter production. Thus, the situation is such that the effect of leaf photosynthetic activity is likely to be displayed to its maximum extent.

On the other hand, the effect of canopy structure should also be displayed to some extent on maxCGR under these conditions. However, according to our previous results[17] obtained from a number of field experiments using rice plants, the effect of p_0 on the maxCGR becomes apparent when both LAI and solar radiation are at sufficiently high levels. Considering these results together with the present one, canopy structure might be regarded as a secondary factor as compared with p_0, as far as potential productivity in different species is concerned.

In the next place, the relationship of p_0 with the mean CGR for the whole growth duration was examined in the same way as above. Similar but less clear relationship was obtained between the two as shown in

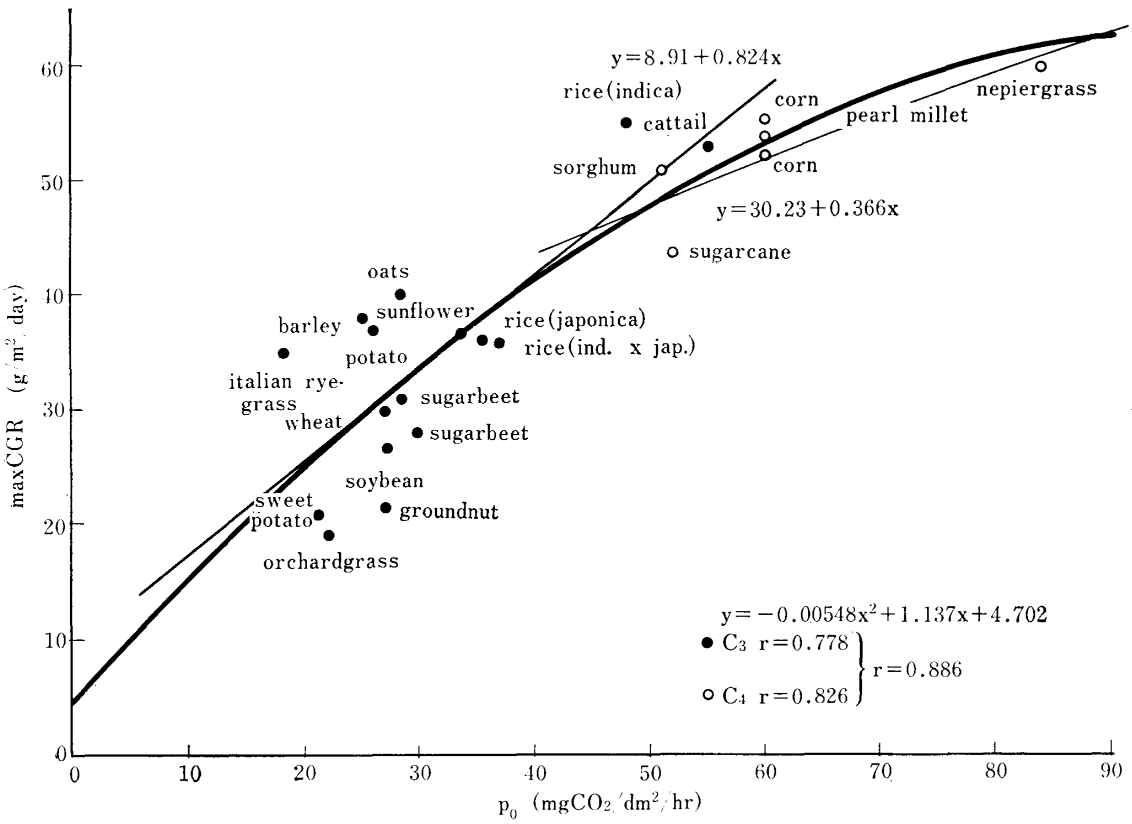

Fig. 1. Relationship of leaf photosynthetic activity (p_0) with high values in maxCGR among various crop species

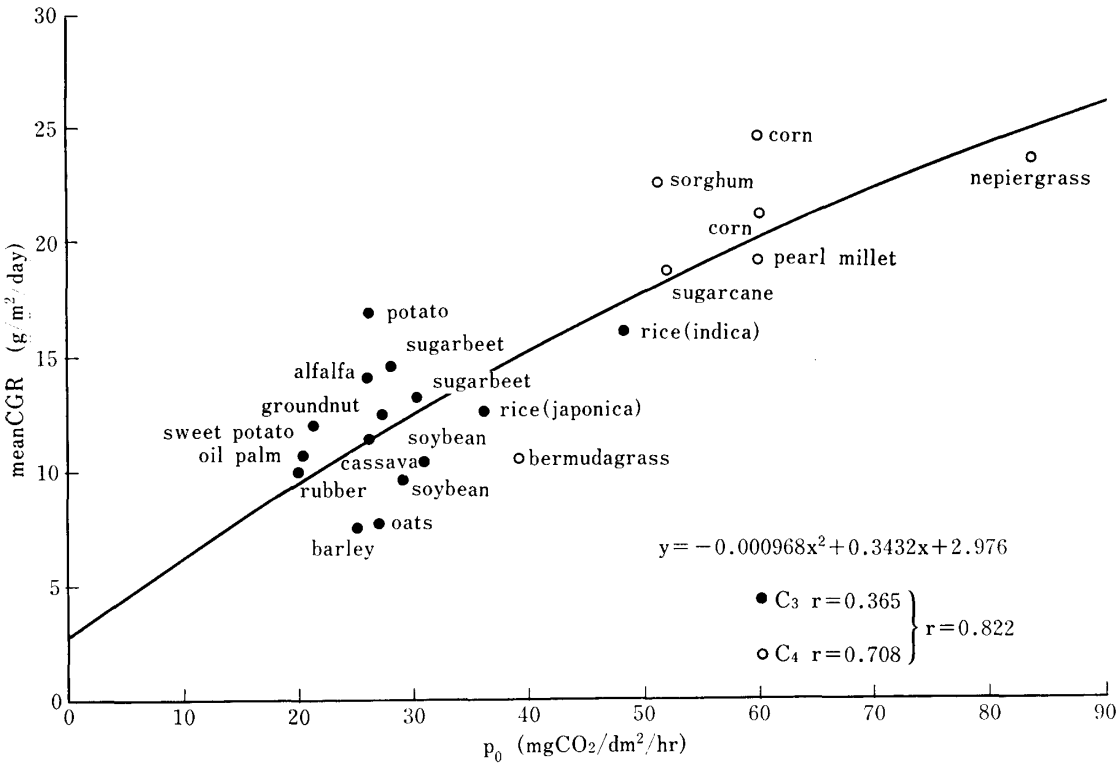

Fig. 2. Relationship of leaf photosynthetic activity (p_0) with high values in mean CGR among various crop species

Fig. 2. Here, the linear correlation coefficient for the C_3 species is very low, but that for the C_4 species is comparatively high, 0.708. The linear correlation becomes as high as 0.822, when the two groups are mixed together. Also a second order regression seems to fit for this relationship.

In this case, however, LAI and its duration should play more important role than in the case of maxCGR and this might be responsible for the lower correlation within each group.

2) *Solar energy utilization efficiency for max-CGR*

In the next place, the efficiency for solar energy utilization, Eu, when the high values in the maxCGR had been observed was compared between the two groups. The difference was not very clear when the Eu values in Table 1 were compared directly, disregarding the difference in solar radiation level, S. It was, however, demonstrated, by correcting the observed values to those at the same radiation level, that the Eu values were higher in the C_4 species than in the C_3 species. The correction was made in the following way:

As the existence of some regression similar to an inverse proportion was anticipated from the equation (1), this point was examined first, using the data of the Maximal Growth Rate Experiments of IBP[18] carried out for 5 years at 7 locations with 2 suitable varieties of rice. Those Eu values when the LAI was higher than 4 in the vegetative phase were picked up and plotted against the solar radiation, S, disregarding the variety, location and season. A linear regression of Eu on S was obtained as indicated in Fig. 3. Similar, linear regression was obtained in soybean (Fig. 4) and sugarbeet (Fig. 5) when the LAI was higher than 3.5 and 3 in the former and the latter, respectively, although no regression was recognized in the case of corn, probably due to the insufficient sample number (Fig. 6).

On the other hand, daily gross photosynthesis of the rice stand was calculated in the same way as IWAKI[8] who employed KUROIWA's equation[12] (2) together with the equation (3):

$$P_g=\frac{2b}{a}\cdot\frac{d}{k}\ln\frac{1+\sqrt{1+akI_m/(1-m)}}{1+\sqrt{1+akI_m\exp(kF)/(1-m)}}\quad\cdots\cdots\cdots\cdots(2)$$

$$I_m=1.031\,S_m+34.3=1.031\frac{2S}{d}+34.3\cdots\cdots(3)$$

where,

a, b: constants characterizing the light-photosynthesis curve of single leaves,
d: daylength, hr, F : LAI,
k: light extinction coefficient,
I_m: daily maximum solar illumination at noon, klx,
S_m: daily maximum solar radiation at noon, ly per hr,
m: light transmissibility of single leaves, and
S: solar radiation, ly per day.

For calculation, the following values were used for parameters:

b=0.215 for C_3 species and 0.32 for C_4 species.

This is based on an unpublished result of A. KUMURA who compared the reported light-photosynthesis curves of various species and gave values of 0.153 and 0.229 as the energy conversion efficiency in photosynthesis for C_3 species and C_4 species, respectively,

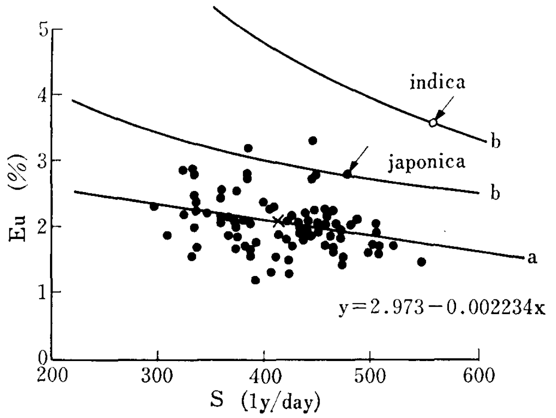

Fig. 3. Regression of the efficiency for solar energy utilization (Eu) of rice stands on solar radiation (S) in the IBP experiments[18]

1) LAI 4, vegetative phase. 2) Arrows indicate the Eu mentioned in Table 1.

a: Linear regression line for the whole data.

b: Theoretical curves calculated by equations (2) and (3).

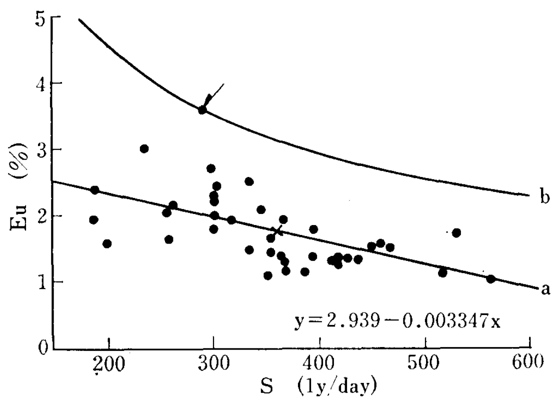

Fig. 4. Regression of Eu on S in soybean stands in the IBP experiments[18]. Symbols are the same as in Fig. 3.

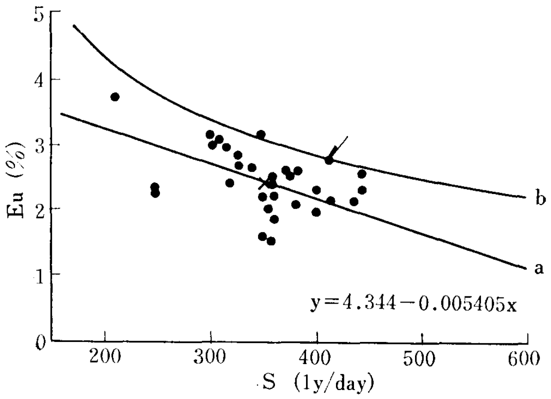

Fig. 5 Regression of Eu on S in sugarbeet stand in IBP experiment[18]. Symbols are the same as in Fig. 3.

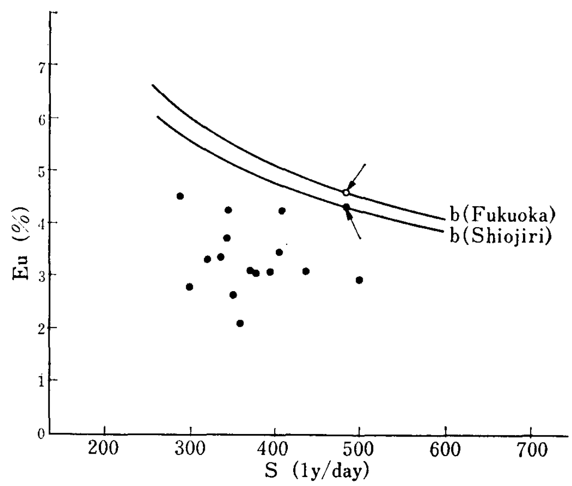

Fig. 6. Regression of Eu on S in corn stands in the IBP experiments.[18] Symbols are same as in Fig. 3.

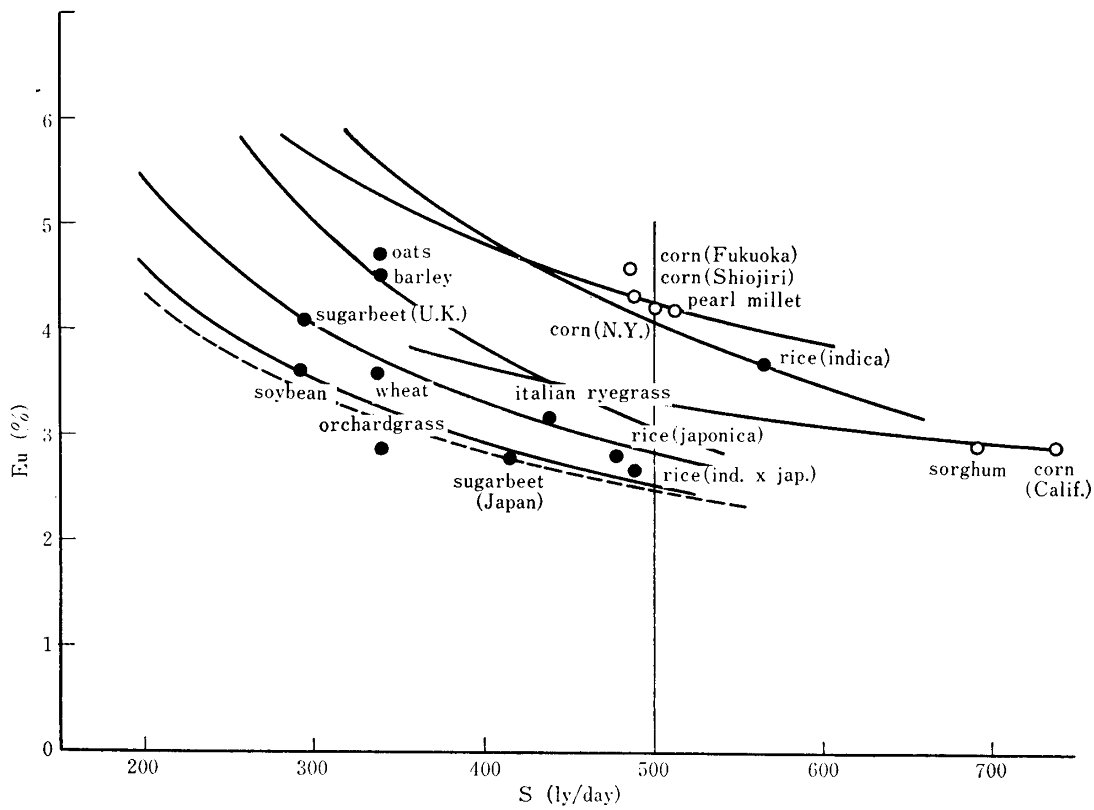

Fig. 7. Theoretical relationships of Eu with solar radiation, S, corresponding to high values in maxCGR

and

$a=b/p_0=0.215/3.6=0.0597$ for *japonica* and

$=0.215/4.8=0.448$ for *indica*, $m=0.9$, $F=6$,

$k=0.34$ (TSUNO and KITAKADO[26]).

A factor of 0.61 was used for conversion of CO_2 to dry matter.

Further assumption was made that respiration was unaffected by solar radiation level within a certain range. Thus, the result of calculation has given the two theoretical curves which pass, as shown in Fig. 3, through the two given points, one for the *japonica* and the other for the *indica*, respectively.

In the same way as above, a theoretical curve was obtained for soybean (Fig. 4), assuming:

$a=b/p_0=0.215/2.7=0.0776$, $d=14$, $F=5$,

Table 3. Comparison among species of solar energy utilization efficiency, Eu, corresponding to the reported high values in the maxCGR, corrected at the same solar radiation of 500 ly/day as shown in Fig. 7.

Species	Eu,%	Species	Eu,%
C_4 corn (Fukuoka, Japan)	4.4	C_3 Italian ryegrass	2.9
〃 (Shiojiri, Japan)	4.1	sugarbeet (U.K.)	2.9
〃 (Calif.)	3.4	〃 (Sapporo)	2.5
〃 (New York State)	4.2	soybean	2.5
pearl millet	4.3	oats	3.3
sorghum	3.3	barley	3.1
mean	3.95±0.43	wheat	2.8
C_3 rice, *indica*	4.1	orchardgrass	2.2
〃, *japonica*	2.8	mean	2.89±0.48
〃, *ind.* x *jap.*	2.7		

$k=0.79$ (KUMURA[11]).

For sugarbeet, it was assumed:

$a=b/p_0=0.215/3.0=0.0717$, $d=14$, $F=5$,

$k=0.94$ (Arbitrarily supposed).

For corn, it was assumed:

$a=b/p_0=0.32/6.0=0.0533$, $d=13$, $F=6$,

$k=0.70$ (MONTEITH[16]).

The results are shown in Figs. 5 and 6. From Figs. 3 through 6, it appears that the theoretical curves may be taken as representing the response of Eu, in its highest values, to different solar radiations. In Fig. 7, the Eu values collected in Table 1 are plotted against the solar radiation, together with these theoretical curves which will enable us to correct the original values to those at the same solar radiation for a more precise comparison of Eu among species. Thus, Table 3 was obtained. Although there is a few exceptions both for C_3 and C_4, the Eu values corresponding to the maxCGR are generally higher in the C_4 than in the C_3 species.

Further, a very close correlation, 0.843, was found to exist between p_0 and the corrected Eu, as shown in Fig. 8. This may be taken to suggest the importance of leaf photosynthetic ability in determining the efficiency for solar energy utilization of crop species in the field.

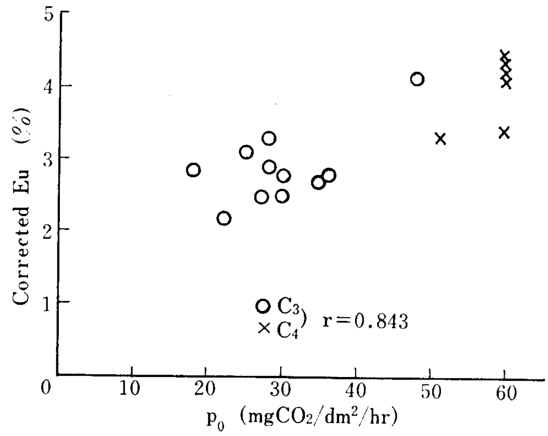

Fig. 8. Correlation between p_0 and corrected Eu.

Summary

Comparison among various crop species was made of the reported high values in the maximum crop growth rate, maxCGR, obtained under very favorable field conditions at various locations in the world, in relation to the reported maximum leaf photosynthetic activity, p_0, observed under natural conditions. Similar comparison was made of the mean CGR. Further, comparison was made of the solar energy utilization efficiency for the maxCGR, taking the solar radiation level into consideration. The following results were obtained:

1) A close second order regression of maxCGR on p_0 seems to exist, including all the available data, regardless of the C_3 and C_4 discrimination. This was interpreted to suggest the outstanding importance of p_0 for determining the species difference in the potential crop productivity.

2) Similar but less close relationship was recognized between the mean CGR and p_0.

3) Solar energy utilization efficiency corresponding to the maxCGR was shown to be higher in the C_4 species than in the C_3 species, with a few exceptions, after correcting the observed values to those at the same solar radiation level. Further, a very close correlation was found between p_0 and the corrected Eu, suggesting the importance of p_0 for determining the efficiency for solar energy utilization of crop species in the field.

Acknowledgement

The author expresses his appreciation to Dr. A. KUMURA for his valuable discussion and kind help, Dr. T. USHIJIMA, Tokyo Univ. of Agriculture and Technology, and Dr. T. TANAKA, Hokuriku Agricultural Experiment Station, for giving permission to cite their unpublished data.

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* In Japanese with English summary, ** in Japanese only.

〔和 文 摘 要〕

作物における最大生産力，葉面光合成能力および太陽エネルギー利用効率

村 田 吉 男
（東京大学農学部）

世界各地で極めて好適な条件の下に栽培された場合にえられた各種の作物の短期間の最大 CGR，および年間の純生産量と生育日数から求めた平均 CGR の高位値を文献から集め，報告された葉面当たりの最大光合成能力（p_0）と比較した．さらに最大 CGR の高位値の得られた場合の太陽エネルギー利用効率（Eu）を，JIBP 地域班によって得られた Eu のデータと黒岩（1968）の式を用いた計算により，同一日射レベルに直して比較した．得られた結果は次のとおりである．

1）最大 CGR は p_0 に対して，C_3 種，C_4 種にかかわらず，全体として密接な一つの曲線回帰を示し，二次回帰で近似した場合，実測値と計算値とは 0.1% レベルで有意な相関（0.896）を与えた．

2）平均 CGR と p_0 の間にも前者の場合よりは弱いが，同様な回帰が認められた．

3）最大 CGR の高位値に対応する Eu 値を，一定日射レベル（500 ly/day）における値に直して比較すると，一，二の例外はあるが，一般に C_3 種より C_4 種の方が高いことが示された．さらに，補正された Eu と p_0 との間には密接な相関（r=0.843, 0.1% レベルで有意）が見られ，太陽エネルギー利用効率の種間差も p_0 に強く依存することが示唆された．