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## I. Introduction

Improvement of crop yields depends on either increasing total dry matter production or increasing distribution of dry matter to grains (13, 53, 92). Dry matter production is closely related to photosynthetic activity of canopy (6, 73, 92). Net photosynthesis has 3 distinct components: the capacity, the amount, and the environment of the photosynthetic surface. The last 2 components are closely related to the morphology of plant, and ultimately of the crop stand, a concept embodied in the term of "plant type."

Increase in rice yields in both temperate and tropical areas, so far, has been associated with changes in the plant type (37, 73, 78, 81, 92). Objectives of varietal improvement to obtain higher yields of rice were plant height for avoidance of lodging, tillering habit for obtaining adequate number of panicles and spikelets, leaf angle for improvement of light environment, reduced sensitivity to photoperiodism, decrease of sterility and so on. The improvement of these characters as well as improved cultivation methods has made a rapid increase of grain yield of rice. From the view point of dry matter production, higher yield of rice attained up to the present is mostly resulted from improvement of photosynthesis of canopy due to improved plant type and structure of canopy. There are reasons to assume that the further gains by this direction of improvement have been ceiling (92). There is however no evidence that yield improvement has been associated with increase in net photosynthesis, although varietal differences in this component are known in many crop species.

Previous studies done on the net photosynthesis will be reviewed. At first with other crops than rice, in 1950 Hasegawa and Wada (27) stated the varietal difference of net photosynthesis in 2 varieties of *Ipomoea batatas* Lam, by measuring carbon dioxide absorbed by alkali (alkali method), although measuring method had not well been established. Fujise and Tsuno (25) observed no difference of net photosynthesis of leaf among 4 varieties of *Ipomoea batatas* by the same method in 1962. Muramoto (49) and El-Sharkawy (18) measured net photosynthesis of leaf in cultivar cotton plant (*Gossypium hirsutum* L. and *Gossypium barbadense* L.) but was unable to recognize any difference. Izhar and Wallace (36) in 1967 found clear difference of net photosynthesis of intact leaves among 5 varieties of *Phaseolus vulgaris* L. by the method of infrared gas analysis of net carbon dioxide exchange and suggested that genetic mechanism controlling the varietal difference in net photosynthesis of leaf is quantitative and that there may be relatively few genes involved according to the result obtained from parents,  $F_1$  and  $F_2$  progenies and backcross ones. Irvine (32) measured leaf photosynthesis of 10 varieties of sugarcane (*Saccharum officinarum* L.) by using  $C^{14}O_2$  and recognized varietal difference ranging from 34.4 to 86.4 mg  $CO_2$  dm<sup>-2</sup> hr<sup>-1</sup>. With maize plant (*Zea mays* L.), Fousova and Avaratovsoukova (22) studied genetic mechanism of photosynthesis by using the leaf disk method based on dry matter increase, extending over  $F_1$ ,  $F_2$ ,  $B_1$ ,  $B_2$  generations and suggested that heterosis of photosynthesis occurred in  $F_1$  generation. Duncan and Hesketh (17) and Heichel and Musgrave (30) recognized clearly varietal difference of photosynthesis in maize by infrared gas analysis, and the occurrence of heterosis in photosynthesis.

In general, photosynthetic efficiency as well as yield of soybean plants (*Glycine max*

L.) are lower than that of *Gramenae* plants (19). There are a lot of studies on photosynthesis of soybean plants intending the improvement of photosynthesis. Ojima and Kawashima (56) and Ojima et al. (57) in 1968 studied varietal difference of photosynthetic efficiency of soybeans and investigated variation and heridity of photosynthetic efficiency over  $F_1$  to  $F_4$  generations. They recognized that there are  $\pm 20\%$  difference in net photosynthetic rate among varieties used and that this character is heritable but no heterosis of this character occurred. Also Curtis et al. (12) recognized varietal difference of this character over a range of 12 to 24 mg  $\text{CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$  among 36 varieties. Dreger et al. (15) obtained the same fact among 9 varieties. Dornhoff and Shibles (14) recognized varietal difference showing significantly higher net photosynthetic rate, over 29.4 to 43.4 mg  $\text{CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ , which had never been obtained in soybean.

According to Stoy (69) there were little differences of photosynthetic efficiency in cultivars of *Triticum*, but Evans and Donstone (20) and Khan and Tsunoda (40) recognized that there are clear differences of net photosynthetic rate among different species of *Triticum* including wild genus.

Apel and Lehmann (1) obtained that the net photosynthetic rate of 115 varieties of barley (*Hordeum vulgare* L.) from different geographical origin indicated a normal distribution over a range of 11–12 mg  $\text{CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ . Seven high yielding varieties of spring barley had approximately uppermost rate of photosynthesis.

Criswell and Shibles (11) indicated significant varietal differences of photosynthetic efficiency in 20 varieties of oat (*Secale cereale* L.), with a high correlation coefficient between 2 successive years in net photosynthetic rate of flag leaves. Carlson (9) recognized 50% difference in net photosynthetic rate between the clone of 2 races of orchard grass (*Dactylis glomerata* L.).

On photosynthesis of rice plant, there were pioneering studies of Mitsui and co-worker (46, 47, 48) and Noguchi (54, 55) in late 1930's. Mitsui and co-worker examined the influences of measuring condition such as light, temperature, carbon dioxide concentration and so on, in order to establish the measuring method by adopting the alkali method, so that they were able to obtain relatively higher rate over 30 mg  $\text{CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$  under natural light condition. Nagao (52) recognized a difference in photosynthetic rate of 2 rice varieties by dry matter increase in leaf disk.

During 1950's, Yamada et al. (90) developed a new apparatus for measuring photosynthetic rate by alkali method which made it possible to promote further studies on photosynthesis of rice. Murata (50, 51) recognized varietal differences of photosynthetic rate over a range of 9.9–12.6 mg  $\text{CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$  and  $\pm 20\%$  of mean rate at the active tillering stage among 30 varieties of rice during his early studies. Osada and Murata (59, 60) measured photosynthetic rate of 12 varieties of rice at the seedling and active tillering stage for 7 times in 2 years by using infrared gas analyzer. From the above experiments, they recognized varietal difference of photosynthetic rate in rice. However, Murata's data obtained from detached leaves of rice showed rather lower rates of about 10 mg  $\text{CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ , whereas Osada gave relatively higher rates of about 20 mg  $\text{CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$  at the seedling stage and 10–15 mg at the active tillering stage. No significant mutual correlation between these experiments was obtained except one case. There still remained some discrepancies from above experiments in inferring the existence of real varietal difference of photosynthetic efficiency in rice. Hayashi (29) recognized significant difference of net assimilation rate among 14 varieties of *Japonica* and 4 varieties of *India* rice.

IRRI (33) obtained much higher rate of photosynthesis with the range of 34.5–62.1 mg CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup> and mean rate of 46.6 mg with 50 varieties of rice including few *Japonica* varieties of the tropics than had ever obtained, although these values were not reproduced in the succeeding experiments with the same varieties (72). Takano and Tsunoda (71) obtained net photosynthetic rate over a range of 20 to 40 mg CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup> among *Japonica* and *Indica* type and wild rice and indicated the quadratic regression between net photosynthetic rate and nitrogen content per leaf area. McDonald et al. (44) inferred that rate of photosynthesis was 67.4 mg CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup> and heterosis of photosynthetic rate occurred with relatively higher heritability.

Thus, it has been clarified that there are varietal differences of photosynthetic rate of single leaf in many crop species and genus. There are, however, only few papers showing that photosynthesis of single leaf relates directly to grain yield, although the former is a basic element of photosynthetic rate of whole crop canopy. According to Murata (51), during the vegetative growth stage except an extremely early stage, rate of dry matter increase of rice canopy related positively to net assimilation rate which related positively to photosynthetic rate of rice canopy. There was, however, no relation between photosynthetic rate of single leaf and that of rice canopy, to which light-receiving efficiency related positively. Contrary to this during the ripening stage of rice, the rate of dry matter increase related positively to photosynthetic rate of single leaf. These results indicated that dry matter production was influenced by the size of leaf area before the occurrence of mutual shading and then after the mutual shading occurred the light-receiving efficiency became to be a dominant factor affecting dry matter production. It is in the period of decreasing leaf area during the ripening stage that photosynthetic rate of single leaf effect dominantly dry matter production. Osada (61) recognized many cases showing the significant positive relationship between photosynthetic rate of single leaf and relative growth rate but it was a rare case that photosynthetic rate of single leaf is related to the rate of dry matter increase. On the other hand, Loomis and Williams (42) suggested based on the theoretical equation of dry matter production of canopy that photosynthetic rate of single leaf is an influential factor determining the rate of dry matter increase. Buttery (6) indicated experimentally that the difference of the rate of dry matter increase was resulted from that of net assimilation rate based on growth analyses of maize and soybean. Irvine (32) obtained photosynthetic rate of single leaf related positively to yield of culm weight of sugarcane. There are some papers in which the relationship between photosynthetic rate and grain yield is recognized indirectly with spring barley and soybean. With spring barley, high yielding varieties were omnipresent in higher side of frequency distributoin of photosynthetic rate of single leaf (1). In soybean, high yielding varieties such as Crosby, Amosoy, Hark and Harosoy showed higher photosynthetic rate of single leaf (14). However, there are examples showing no relationship between photosynthetic rate of single leaf and grain yield with soybean (12), perennial ryegrass (*Lolium perene* L.) (65) and barley (2). Watson (84) and Hanson (26) suggested that leaf area affected dominantly grain yield in maize and few other crops. Furthermore, it was recognized with barley and wheat that grain yields were connected intimately to photosynthetic area above flag leaves including ears (67, 74, 82, 87, 91). Duncan and Hesketh (17) reported that there were no differences in photosynthetic rate among maize cultivars originated from different altitudes and their yields were influenced by the size of leaf area. As given above there are some contradictions regarding the relationship between photosynthetic rates of single

leaf and grain yields of many crops.

In the studies on photosynthetic rate, the accuracy of measuring photosynthesis has been increased remarkably due to the improvement of measuring apparatus from alkali method to infrared gas analysis and of measuring techniques from the detached leaf method to attached leaf method using improved chambers. Therefore, in studies during late 1950's and early 1960's, it is very likely that only a fraction, if not a small fraction, of actual photosynthetic rate was measured and on which varietal differences were discussed. In late 1960's, it was made possible to obtain definitely higher rate of photosynthesis, namely, 50 mg CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup> in rice, 35 mg in soybean and 28–85 mg in maize. Therefore, it is necessary to reinvestigate the problem of photosynthetic efficiency of rice in relation to varietal differences and grain yields.

The objectives of the present study are (i) to find out varietal differences of photosynthetic efficiency of *Indica* rice by determining net assimilation rate in growth analysis and net photosynthetic rate by the infrared gas analysis, and to find varieties with higher photosynthetic efficiency as gene sources for further improvement of rice plants and (ii) to establish physiological criteria for selecting varieties (iii) to evaluate the contribution of varietal difference of photosynthesis to dry matter production.

## II. Discussion on methods to be applied

Net photosynthetic rate can be measured accurately, over a short time interval, by the use of an infrared gas analyzer. A large number of genotypes may thus be screened in a short time with relatively few replication. But the method measures only the net CO<sub>2</sub> exchange of single leaf just after matured under a set of environmental condition—under condition of light saturation, optimal temperature and saturated water vapour pressure, etc. The results may be influenced by the type of enclosure used. On the other hand, measurements based on dry weight change over longer time intervals—days or weeks—require a large number of plants, because enough amount of material is needed to detect accurately the dry weight change and the replication is necessary to deal with plant variability. Since a large number of genotypes must be tested concurrently, this method requires much more time than the first method. Growth analysis, however, has the advantage of giving an integrated measurement of net photosynthetic activity over the wide range of conditions that prevail in the field. Therefore, this measurement may be more realistic than one obtained under a set of arbitrary conditions. It is true that dry weight measurement of whole plants over long periods may involve some effect of canopy structure. But if young isolated plants are used, this effect is probably negligible.

For those reasons, the author decided to make preliminary measurements by standard growth analysis (41, 64) on relative growth rate (RGR), net assimilation rate (NAR), and leaf area ratio (LAR) as follows:

$$\text{NAR} = \frac{W_2 - W_1}{L_2 - L_1} \times \frac{\log_e(L_2 - L_1)}{t_2 - t_1} (\text{mg} \cdot \text{dm}^{-2} \text{ leaf area} \cdot \text{day}^{-1})$$

$$\text{LAR} = \frac{1}{2} \left( \frac{L_1}{W_1} + \frac{L_2}{W_2} \right) (\text{cm}^2 \cdot \text{g}^{-1})$$

$$\text{RGR} = \frac{\log_e(W_2 - W_1)}{t_2 - t_1} (\text{mg} \cdot \text{g}^{-1} \cdot \text{day}^{-1})$$

$$\text{SLW}_1 = \frac{\text{LW}_1}{\text{L}_1} (\text{mg} \cdot \text{cm}^{-2})$$

$$\text{SLW}_2 = \frac{\text{LW}_2}{\text{L}_2} (\text{mg} \cdot \text{cm}^{-2})$$

$$\text{SLW}_{\text{pn}} = \frac{\text{LW}_{\text{pn}}}{\text{L}_{\text{pn}}} (\text{mg} \cdot \text{cm}^{-2})$$

where

- $W_1$  : total dry weight of shoot at the first sampling time
- $W_2$  : total dry weight of shoot at the second sampling time
- $L_1$  : total leaf area at the first sampling time
- $L_2$  : total leaf area at the second sampling time
- $t_1$  : date of the first sampling time
- $t_2$  : date of the second sampling time
- $\text{LW}_1$  : total leaf weight at the first sampling time
- $\text{LW}_2$  : total leaf weight at the second sampling time
- $\text{LW}_{\text{pn}}$  : leaf weight of leaves in which  $P_N$  was measured
- $\text{L}_{\text{pn}}$  : leaf area of leaves in which  $P_N$  was measured

Nevertheless, if NAR is in fact strongly related to the more easily measurable net photosynthetic rate of leaves per unit leaf area ( $P_N$ ), then this latter simple determination will suffice. Therefore, the author decided to screen a wide range of genotypes by growth analysis and then compare NAR and  $P_N$  with selected ones. The leaf characteristics (specific leaf weight, SLW, and nitrogen content per unit leaf area and so on as above mentioned) were also examined as the possible indices of photosynthetic capacity which are measured by the growth analysis and  $\text{CO}_2$  exchange method.

### III. Net assimilation rate and its related plant characters of rice varieties

#### 1. Effect of growth stage and spacing of plants in pot experiment on growth analysis

Net assimilation rate (NAR) obtained under the environmental condition without mutual competition within and among isolated plants is the manifestation of photosynthetic capacity of each variety under a given climatic condition. In this section, effects of growth stage and spacing on net assimilation rate were examined in order to find out the experimental condition for growing plants without causing mutual competition at an early tillering stage when experiment can be performed relatively easily.

##### (1) Materials and methods

Varieties: An improved variety, IR8, and a traditional variety, Emata A 16-34 of India, were used. IR8 has a semi-dwarf culm and dark green elect leaves. Emata A 16-34 has a long culm, pale green and droopy leaves and large leaf area per leaf. In short, both varieties have comparable characters in growth habit.

Method of growing plants: Porcelain Wagner pots (a/2000)<sup>1)</sup> containing Mahaas

<sup>1)</sup> a/2,000, a/5,000 porcelain Wagner pot: a is 100 m<sup>2</sup> or ha/100.

clay soil were used. Soil was acidified to pH 5.5–5.8 with sulfuric acid (0.5 ml of conc.  $\text{H}_2\text{SO}_4/\text{kg}$  dry soil). After puddled, soil was allowed to stand over night, and ammonium sulfate, superphosphate and potassium chloride were applied ( $\text{N-P}_2\text{O}_5\text{-K}_2\text{O}$ : 1.5-0.8-1.0 g/pot.) In the experiment on growth stage, 20 seedlings were transplanted to a pot at the second leaf stage. Ten plants per pot were harvested as the first sampling 10 days after transplanting and other 10 plants as the second sampling 7 days after the first sampling. Additional samplings were made 2 days after the first and second samplings. As a result, samples at 5 different leaf stages from 4.8 leaf age to 7.8 leaf age (Table 1) were obtained for the measurement of net assimilation rate. In the spacing experiment seedlings of the second leaf age were planted at a rate of twice of intended number of seedlings per pot, and at the first sampling at 12 days after planting a half of the seedlings was harvested from each pot. As a result, the spacing of 3, 5, 10, 15 and 20 plants per pot was obtained. Pots were arranged with an adequate spacing not causing mutual competition among pots by randomized method with 3 replicates on the lawn at the International Rice Research Institute. Plant samples were taken at 7 to 8 a.m. at each sampling. In the growth stage experiment, leaf blade of 3 of 10 plants was removed from leaf sheath for measuring leaf area by automatic leaf area meter model AAM-1 (Hayashi Denkoh, Co.). Residual sheaths and 7 plants were used for measuring dry weight after oven-dry at  $80^\circ\text{C}$  for 3 days. Total leaf area was calculated from observed leaf area with the rating method (83). In the spacing experiment, leaf blades of 3 out of each number of plants in each spacing were measured for leaf area. Other experimental procedures were the same as that in the growth stage experiment.

## (2) Results and discussion

Table 1 shows the effect of growth stage and spacing on net assimilation rate. Solar

**Table 1 Effect of growth stage and spacing on NAR in pot experiment (1972).**

Experimental duration	Spacing (No. of plant/ pot)	IR 8			Emata A 16—34		
		Leaf stage <sup>2)</sup>	No. of increased leaves	NAR mg dm <sup>-2</sup> day <sup>-1</sup>	Leaf stage	No. of increased leaves	NAR mg dm <sup>-2</sup> day <sup>-1</sup>
1) Growth stage <sup>4)</sup>							
i) April 7—14	10	4.8—7.2	2.4	105.2 bc <sup>3)</sup>	4.0—6.1	2.1	117.2 b
ii) April 9—16	10	5.5—7.8	2.4	115.4 b	4.7—6.7	2.0	122.8 b
iii) April 11—18	10	6.2—8.2	2.0	98.8 bc	5.2—7.2	2.0	108.5 c
iv) April 13—20	10	6.8—8.4	1.7	159.3 a	5.9—7.7	1.9	180.0 a
v) April 15—22	10	7.4—8.9	1.6	92.6 c	6.4—7.9	1.6	99.5 c
2) Spacing							
April 9—16	3	5.4—8.0	2.6	97.6 b	4.7—6.8	2.1	106.0 b
"	5	5.4—7.7	2.2	116.6 a	4.8—6.9	2.1	116.0 a
"	10	5.5—7.8	2.4	115.4 a	4.7—6.7	2.0	122.8 a
"	15	5.6—7.7	2.1	88.6 b	4.7—6.7	2.0	101.5 b
"	20	5.4—7.7	2.2	90.1 b	4.7—6.5	1.7	91.0 c

1) Spacing in a/2000 size of porcelain pot: plants/pot.

2) Leaf stage at the first and the second samplings.

3) Duncan's multiple range test at 5 %.

4) Solar radiation and mean temperature, April 7—14: 460  $\text{ly day}^{-1}$  and  $25.9^\circ\text{C}$ , April 9—16: 437 and  $26.9^\circ\text{C}$ , April 11—18: 497 and  $27.6^\circ\text{C}$ , April 13—20: 540 and  $27.9^\circ\text{C}$ , April 15—20: 616 and  $27.7^\circ\text{C}$ .

**Table 2 Analysis of variance on NAR in Table 1.**

Source	df	ss	ms	F
(IR 8 growth stage)				
Total	14	9689.34		
Treatment	4	8467.99	2116.99	13.964**
Block	2	8.533	4.267	0.0281 <sup>ns</sup>
Error	8	1212.81	151.60	
(Emata A 16—34 growth stage)				
Total	12	12661.61		
Treatment	4	12032.32	3008.07	77.120**
Block	2	317.20	158.60	4.065 <sup>ns</sup>
Error	8	312.10	39.013	
(IR 8 spacing)				
Total	14	2907.60		
Treatment	4	2222.93	555.73	15.086**
Block	2	283.60	141.80	2.829 <sup>ns</sup>
Error	8	401.07	50.13	
(Emata A 16—34 spacing)				
Total	14	1963.60		
Treatment	4	1815.69	453.90	25.008**
Block	2	2.8000	1.4000	0.0771 <sup>ns</sup>
Error	8	145.20	18.150	

radiation fluctuated during the period of growth stage experiment as indicated in foot notes. It was below  $500 \text{ cal cm}^{-2} \text{ day}^{-1}$  in the stage (i) to (iii), but beyond  $500 \text{ cal}$  in the stage (iv) and (v). Net assimilation rate at the stage (iv) was excluded because it was assumed that the net assimilation rate was increased extremely due to higher solar radiation at that stage. Analysis of variance given in Table 2 shows that there are significant differences between treatments but insignificant differences between blocks in both experiments. Therefore, as shown in Duncan's range test (16), IR8 showed higher NAR in the stage (ii), namely, the leaf stage of 5.5–7.8 in the period from 9 to 16, April. Emata A 16–34 also showed higher NAR in the stage (i) and (ii) namely, the leaf stage of 4.0–6.1 and 4.7–6.7 in the period from 7 to 14 and 9 to 16, April. Table 3 shows, significant difference in leaf emergence rate which decreased as leaf age increased. Analysis of variance of leaf growth, given in Table 4, shows insignificant difference between blocks and significant one between treatments. IR8 had higher leaf emergence rate at the stage (i) and (ii) in the period from 7 to 14 and 9 to 16, April and Emata A 16–34 had higher rate at the stage (i) in the period from 7 to 14, April.

From the result of above experiments the criterion of the growth stage for the first sampling is considered to be 5.5 leaf age for IR8 and 4.7 leaf age for Emata A 16–34. There exist the effect of spacing on net assimilation rate as shown in Table 1. Higher NAR was obtained at spacing of 5 and 10 plants per pot in both varieties. The leaf emergence rate decreased as spacing increased in this experiment. This fact confirms that there was no mutual interference among plants at the spacing of 5–10 plants per pot at this stage, so that each of them can be regarded as an isolated plant.



**Table 3 Rate of leaf emergence at different growth stage.**

Replicates	Leaf emergence rate <sup>4)</sup>				
	Apr. 7—14	Apr. 9—16	Apr. 11—18	Apr. 13—20	Apr. 15—20
(IR 8)					
1	2.49 <sup>1)</sup>	2.37	1.98	1.60	1.69
2	2.35	2.45	2.03	1.56	1.52
3	2.42	2.22	1.92	1.86	1.49
Mean	2.42	2.35	1.98	1.67	1.57
	a <sup>2)</sup>	a	b	bc	c
Initial and final growth stage by leaves <sup>5)</sup>					
	4.75—7.17 <sup>3)</sup>	5.47—7.82	6.24—8.22	6.76—8.44	7.36—8.93
(Emata A 16—34)					
Leaf emergence rate					
1	2.18	2.01	1.91	1.73	1.53
2	2.21	2.09	2.05	1.88	1.59
3	1.91	1.92	1.95	1.92	1.53
Mean	2.10	2.01	1.97	1.84	1.55
	a	ab	ab	b	c
Initial and final growth stage by leaves					
	4.04—6.13	4.70—6.71	5.21—7.18	5.85—7.70	6.38—7.93

- 1) Mean of 10 seedlings.
- 2) Duncan's multiple range test at 5 %.
- 3) Leaf growth stage of the first and the second samplings.
- 4) The increase of leaf number during experiments.
- 5) Growth stage as expressed by number of leaves born on the main culm.

**Table 4 Analysis of valiance on leaf growth.**

Source	df	ss	ms	F
(IR 8)				
Total	14	0.72942		
Treatment	4	0.59600	0.14900	15.664**
Block	2	0.05733	0.02867	3.014 <sup>ns</sup>
Error	8	0.07610	0.009512	
(Emata A 16—34)				
Total	14	1.94923		
Treatment	4	1.80267	0.45067	12.596**
Block	2	0.00933	0.00467	0.130 <sup>ns</sup>
Error	8	0.28623	0.03578	

Thus, the optimum stage for the first sampling for net assimilation rate is the 5th leaf age for IR8 and the 4th leaf age for Emata A 16—34 because leaf emergence rate of IR8 was larger than that of Emata A 16—34. Since number of days required to reach the given leaf age is different with seasons, IR8 was used as an index variety.

In summary, to determine net assimilation rate using a group of plants but under the environment of isolated plants, the following conditions are needed; (i) IR8 is utilized as an index variety for the leaf age (ii) IR8 and experimental materials are transplanted to porcelain Wagner pots with the size of a/2000 at a rate of 5–10 plants per pot at the 2nd leaf age, (iii) the first sampling be made at the 5th leaf age and the second sampling 7 days after the first sampling.

## 2. Varietal difference of net assimilation rate

Adopting the experimental condition mentioned above, which is required to measure the net assimilation rate under the environment of isolated plants, the net assimilation rate of a large number of rice varieties was determined to know whether varietal differences in the net assimilation rate actually exist or not, and to know effects of climatic environment during growth period on net assimilation rate.

### (1) Materials and methods

It is presumed that high photosynthetic capacity is likely to be found among vigorous traditional varieties of *Indica* rice. Vigorous growth is considered to be one of genetic characters (59) and the large variability may be shown among *Indica* rice varieties. Therefore, from the “catalog of rice cultivars and breeding lines in the world collection of IRRI 1970” (34), the author selected all the varieties that have characteristics indicative of vigorous growth: long culm (more than 120 cm), high tillering ability (more than 30 tillers), and thick culm (more than 6 mm). These varieties were classified into 3 groups depending on the leaf color intensity (group A, pale green; B, green; C, dark green) which may possibly be related to photosynthetic capacity. And group 4 was varieties with other miscellaneous characteristics. Table 5 describes the experimental number, accession number of IRRI, variety name, original country and institution of seed source and variety code (*Indica*, *Japonica* and *Javanica*) of these varieties. Based on the criterion stated above 326 varieties were selected from about 10,000 varieties which IRRI kept at that time. However, a total of 301 varieties were used for the present study, excluding 25 varieties of which enough seeds were not available.

**Table 5 List of varieties selected from “Catalog of rice cultivars and breeding lines in world collection of IRRI 1970”.**

A series of classification factors (1-120-30-6)

Exptl. var. no.	Accession no.	Variety name	Seed source**	Origin**	Variety***
A 1	3707	ANIFROM N. POKHARA	92-5	42	1
2	4919	BAMBAKO	197-1	58	1
3*	33	BENGAWAN	73-2	44	1
4	6803	B-38-35	13-1	13	1
5	7073	VHAU BA IN	97-3	14	1
6	7057	GAN DA SOM	97-3	97	1
7	7227	KESORN 4416 D	97-3	86	1
8	648	KHAO BAN DON	73-2	86	1
9	7855	KHAO POODHAT	58-1	86	1
10	812	KORIKIT	73-2	73	1
11	714	MALAMAN	73-2	73	1
12	4911	MALEFIKI	107-1	58	1

13	539	MINABIR 2	72-1	72	1
14	701	MTV 19	73-2	42	1
15	7103	NANG CO LOT L 41	97-3	97	1
16	231	NANG DUM TO	97-1	97	1
17	7875	NH 2	107-1	107	1
18	762	PERURUTONG NB	73-2	73	3
19*	581	PILIT MORADO	73-2	73	1
20	8113	P. QILOKO BINAYAMBAN	73-12	73	1
21	1568	PU CHIANG HS IAO CHIU KU	92-5	20	1
22	832	PW 256	86-3	86	1
23	5913	RANDIN CHINA 4	42-47	57	1
24	5240	RAMILON	73-8	73	1
25	698	SALAK	73-2	44	1
26	556	SLO 1	73-2	42	1
27	641	SLO 14	73-2	42	1
28	637	SLO 17	73-2	42	1
29	7244	SOC RANG	97-3	97	1
30	6711	WHITE CHINA	29-1		1
31	5799	WRC 2	42-60	42	1
32	715	10022	73-2	42	1

## B series of classification factors (2-120-30-6)

Exptl. var. no.	Accession no.	Variety name	Seed source	Origin	Variety
B 1	180	ADDAY LOCAL SEL.	42-45	42	1
2	5901	ADT 22	42-47	42	1
3	7128	AKP 11	97-3	42	1
4	5132	AMBARIKORI	73-8	2	1
5	4184	ANADARA	21-8	44	1
6	8	ANAK NAGA	57-1	57	1
7	7252	ANG KRANG	97-3	14	1
8*	6361	ANTERSAL 67	42-47	42	1
9	4164	BAKO	21-8	44	1
10*	9815	BAM 9	21-8		1
11	7876	BANDIOULOU	58-1	34	1
12	7230	BANG PRA 281	97-3	86	1
13	6160	BANKURA 31	42-47	42	1
14	8327	BANSFUL	67-3	67	1
15	630	BAOK	73-2	44	1
16	7062	BA THAC NHO	97-3	97	1
17	3603	BENGAWAN	92-5	44	1
18	3609	BENGAWAN	92-5	44	1
19	3616	BENGAWAN 2794	92-5	44	1
20	4162	BENGGALE	21-8	44	1
21	3617	BENONG 130	92-5	44	1
22	7935	BEN SALAY	107-1	107	1

23	7891	BEREKUTE	107-1		1
24	624	BHASMANIK	73-2	42	1
25	4192	BOELO	21-8	44	1
26	591	BOLAO	73-2	73	1
27	7056	CADUNG KET SOM	97-3	97	1
28*	7197	CADUNG SA 70-1729	97-3	97	1
29	7149	CADUNG TRANG	97-3	97	1
30	7249	CADUNG TRANG POP	97-3	97	1
31	7065	CAO CO	97-3	97	1
32	819	CARISSI	73-2	73	1
33	7222	CATETO DOMADO	97-3	92	1
34	5944	CHANGUA PROEUM K 112	42-47	14	1
35	1131	CHAO HSIEN KENG	92-5	20	1
36*	7191	CHAO LY NGOC	97-3	97	1
37	4312	CHUN 12-606	21-8	20	1
38	4313	CHUN 41-25	21-8	20	1
39	4317	CHUN 109-11	21-8	20	1
40	7821	CH 18×MAS M 24 (2126)	58-1	17	1
41	6186	CO 2	42-47	42	1
42	6669	CONCHERI	42-46	76	1
43	6686	COTMIRSAL	42-46	76	1
44	6323	CPY 19	42-47	17	1
45	9809	CR 2001	21-8		1
46	6212	CROSS 116	42-47	42	1
47	647	C 47-43	73-2	44	1
48	5855	DA 5	42-47	67	1
49	7535	DOND UNI KUNLUZ	92-5	1	1
50	6199	D 52/37	59-1		1
51	4917	D 99	107-1	35	1
52*	7921	EBANDIAUL YAFITE	58-1	80	1
53	8187	EMATA A 16-34	21-3	42	1
54	7910	ETOMOLONG	58-1	80	1
55	4913	FAYA	107-1	58	1
56	8887	FR 13 A	42-47	42	1
57	1591	FU TAO YI	92-5	20	1
58	4908	GANGTANG	107-1	66	1
59	4229	GENDJAH BANTEN	21-8	44	1
60	4962	HAI TUNG SHEN-LI	73-8	21	1
61	26	HAJI HAROUN	57-1	57	1
62	5548	HAU	73-2	21	1
63	5898	HBJ AMAN V	42-47	67	1
64	7940	HBJ 1	58-1	42	1
65	5859	HNANWA PHINGAUK A 26-2	42-47	13	1
66	7903	HINANWA PHINGAUK A 36-3	58-1	17	1
67	5942	HONG×01 B R 31	42-47	97	1
68	4933	HR 8	107-1	42	1
69	820	INASLUNA	73-2	73	1

70*	7932	INDOCHINA 53	107-1	107	1
71	6633	JAMBABAM VERMELHO	76-2		1
72	864	JAO HAWN 32-18-44	86-3	86	1
73	9836	JBS 236	42-47	42	1
74	9837	JBS 279 (M)	42-27	42	1
75	9839	JBS 377 B	42-47	42	1
76	9841	JBS 524	42-47	42	1
77	9838	JBS 1172	42-47	42	1
78	8336	JHINGASAIL	67-3	67	1
79	8221	JW 24	21-3	42	1
80*	9126	JW 77	21-3	42	1
81	6195	KADING THNG	59-1		1
82	948	KAHOGO	52-1	52	1
83	6613	KALIMEKRI 77/5	67-5	67	1
84	7750	KALUHEENATI	17-4	17	1
85	9768	KANAKJI	29-1		1
86	8904	KATHARAMANA	17-4	17	1
87	4915	KAV 12	107-1	58	1
88	4173	KEKE KALA	21-8	44	1
89	6689	KENDAL PEQUENO	42-46	76	1
90	6121	KHAO BHUDAT	42-47	86	1
91	841	KHAO MED LEK 4-16-36	86-3	86	1
92	853	KHAO NAM KAHNG 82	86-3	86	1
93	174	KHAO TAH HAENG 17	86-3	86	1
94	847	KHAO TAH OO	86-3	86	1
95	7221	KHAO TOT LONG 227	97-3	86	1
96	5861	KHA YANGYA DA 34-181	42-47	13	1
97	8326	KHIRAJALI	67-3	67	1
98	5133	KIHOGO	73-8	85	1
99	7248	KONG MARETH 4 T T	97-3	14	1
100*	7752	KOTANAVALU	17-4	17	1
101	7130	KRACHAK CHROUK	97-3	14	1
102	9764	KRS 1	29-1	29	1
103*	6442	LAMBAYAQUE 1	42-47	72	1
104	6176	LATISAIL (DACCA 17)	42-47	42	1
105	651	LEUANG YAI 344	73-2	86	1
106	838	LEUANG 28-1-8	86-3	86	1
107	861	LEUANG 28-1-47	86-3	86	1
108	7094	LUA GAO	97-3	97	1
109	7169	LUA MEN	97-3	97	1
110	865	LUANG PRATAHN 54-7-28	86-3	86	1
111	7150	LUA SOI	97-3	97	1
112*	7147	LUA TIEU HA NOI	97-3	97	1
113	7101	LUA TRANG	97-3	97	1
114	7092	LUA XIEM	97-3	97	1
115	598	LUBANG	73-2	73	1
116	7233	LUENG ON TONG PRATAN 408	97-3	86	1

117	6108	MADAEL 39 MY 137	42-47	17	1
118	709	MADRID	73-2		1
119	376	MAKALIOKA	56-1	56	1
120	381	MAKALIOKA PRECOCE	56-1	56	1
121	9900	MALATI	67-3	67	1
122	601	MALIGAYA	73-2	73	1
123	7934	MAMOSSOU	58-1	34	1
124	821	MARINIS	73-2	73	1
125	3605	MAS	92-5	44	1
126	7889	MATINI	58-1	34	1
127	5834	MAURITIUS LOCAL	42-47	104	1
128	5914	MAYANG EBOS 80	42-47	57	1
129	5903	MAYANG SAGUMPAL	42-47	57	1
130	5220	MITAO	73-8	73	1
131	7906	MIYC 407	58-1	17	1
132	7897	MLYC×VI 283	58-1	65	1
133	617	MODBOD NGA I TOM	73-2	73	1
134	6114	MOLAGA SAMBA G 18	42-47	17	1
135	773	MONTENEDO	73-2	73	1
136	4167	MONTIA MENGI	21-8	44	3
137	4178	MONIJA	21-8	44	3
138	4161	MONIJA NAQ	21-8	44	1
139	650	MTV 1	73-2	42	1
140	654	MTV 2	73-2	42	1
141	671	MTV 6	73-2	42	1
142	616	MTV 7	73-2	42	1
143	6031	MTV 8	42-47	42	1
144	664	MTV 11	73-2	42	1
145	6365	MTV 15	42-47	42	1
146	7912	MTV 17	58-1	42	1
147	6376	MTV 20	42-47	42	1
148	176	MVEY NAWNG 62	86-3	86	1
149	5935	MWESWE A 29-212	42-47	13	1
150*	7915	NAANG SAMBEY	58-1	14	1
151	7901	NALLU MOLLI KARUPPAN	58-1	65	1
152	7235	NAM DOK MAI 9	97-3	86	1
153	7058	NANG BANG SOM	97-3	97	1
154	5957	NANG KEO R 138	42-47	97	1
155	7183	NANG LE	97-3	97	1
156	7110	NANG MAU	97-3	97	1
157*	7051	NANG NGUOT TRANG	97-3	97	1
158*	7052	NANG RUM TRANG	97-3	97	1
159	230	NANG TAY C	97-1	97	1
160	7916	NANG TAY NHO CE 15	58-1	97	1
161	7095	NAP MV-V	97-3	97	1
162	5930	NGASEIN C 21-04	42-47	13	1
163	857	NIAW SAN PAHTAWNG	86-3	86	1

164	9765	N Z RICE	29-1		1
165*	6731	PADANG TRENGGANU	57		1
166	8259	PADI RAOEKANG	21-3	44	1
167	610	PANGASINAN	73-2	73	1
168	6574	PANKIRAJ 258	67-5	67	1
169	8912	PANNETI	17-4	17	1
170	677	PATNAI 23	73-2	42	1
171	6252	PAUNG MALAUNG (3)	42-47	17	1
172	8238	PEH-KU	21-3	21	1
173	6177	PERILLANEL 26014	42-47	17	1
174*	35	PETA	73-2	44	1
175	3606	PETA	92-5	44	1
176	5235	PILIMAR	73-8	73	1
177	7728	PODIMAWEE	17-4	17	1
178	7710	PODISAMBA A-8	17-4	17	1
179*	7913	POKKALI 2	58-1	17	1
180	6215	PTB 2	42-47	42	1
181	8251	PTB 5	21-3	42	1
182	6274	PTB 9	42-47	42	1
183	7816	PUNASA KONOMANI	58-1	59	1
184	7829	QUINDOUN	58-1	59	1
185	6729	RADIN CHE ALI	57-	57	1
186	10	RADIN CHINA 4	57-1	57	1
187	6278	RADIN EBOS 33	57-	57	1
188	7861	RADIN EBOS 33	58-1	57	1
189	9538	RAMANI	63-1	63	1
190	8913	RATHKUNA	17-4	17	1
191	7126	SOS SUCON 129	97-3	86	1
192	8233	RTS 5	21-3	97	1
193	6205	R 10	42-47	42	1
194	4030	SALAK	92-5	73	1
195*	7229	SAMBOK ANGKRANG	97-3	14	1
196	7909	SAMSEP LEAO	58-1	43	1
197	9882	SAMDRA FENA	67-3	67	1
198	7236	SAR THNGON	97-3	14	1
199	7	SERENDAH KUNING 11	57-11	57	1
200	9	SERENDAH PUTEH	57-1	57	1
201	8242	SHUANG-CHIANG	21-3	21	1
202	115	SIAM	21-7	21	1
203	5915	SIAM 29	42-47	57	1
204	5	SIAM 48	57-1	57	1
205	611	SIGADIS	73-2	44	1
206	6378	SLO 16	42-47	42	1
207	7100	SOC DO×NANG CHET CUT	97-3	97	1
208	4931	SOKOTERA	107-1	100	1
209	9892	SP 12	67-3	67	1
210	9831	SP 20	67-3	67	1

211	5908	SR 26B	42-47	42	1
212	8250	STR 418	21-3	42	1
213	20	SUBANG INTAN 16	57-1	57	1
214	6097	SUBANG INTAN 117	42-47	57	1
215	687	SUKANANDI B	73-2	44	1
216	6116	SULAI 27614	42-47	17	1
217	5960	TAM DEN 516 A	42-47	97	1
218	7194	TAU BAU I	97-3	97	1
219	7173	TAU HUONG A	97-3	97	1
220	7918	TC×M EBOS 80 75/1	58-1	42	1
221	8270	TD 3	21-3	86	1
222	8271	TD 4	21-3	86	1
223*	8273	TD 6	21-3	86	1
224	8276	TD 11	21-3	86	1
225	8201	TD 38	21-3	86	1
226	697	THAILAND	73-2		1
227	5331	TJAHAJA	44-3	44	1
228	7226	TRANOEUP KRASSAING	97-3	14	1
229	8888	T 414	42-47	42	1
230	6146	T 460	42-47	42	1
231	7843	UVAR VELLAI	58-1	17	1
232	7196	VANG LAI	97-3	97	1
233	6322	VELLAI ILLANKALAYAN 28061	42-47	17	1
234	7899	WALA	107-1	107	1
235	1235	WAN KENG III-19-12-59	92-5	20	1
236	5933	YA 97	42-47	13	1
237	6670	XIDDI	42-40	76	1
238	7922	YEMI	107-1	107	1
239	5924	YODAYA A 35-13	42-47	13	1
240	4397	YUN-AN-NIEN-HSU-BIR	21-8	20	1
241	5145	2/16	73-8	85	1
242	161	59-368 (B 11×MAS)	17-1	17	1
243	1595	96-50-1	92-5	20	1
244	1593	97-40-1	92-5	20	1
245	7622	221E/446/2	44-3	44	1
246	389	996	56-1	56	1

## C series of classification factors (3-120-30-6)

Exptl. var. no.	Accession no.	Variety name	Seed source	Origin	Variety
C 1	9252	BALI KAMBANG 37	44-3	44	1
2*	6123	BREAK GANG GAS 836	42-47	44	3
3	5526	BIR-CO-YUAN-LI	21-4	21	1
4	8333	DM 4	67-3	67	1
5	536	EAL 60	72-1	72	1
6	4480	E-HSIN-YAN-SHUN	21-8	20	1
7	870	JAO LEUANG 32-8-11	86-3	86	1



8	8899	MAHARATAWEE	17-4	17	1
9	6403	MTV 18	42-47	42	1
10	7091	NANG CHET CUT	97-3	97	1
11	877	MIAW LEUAD HAED 32-17-28	86-3	86	1
12*	8192	PADI HOJONG	21-3	44	1
13	4421	QUA-ZONE-HUAN-GEN	21-8	20	1
14	181	RAM TULASI	42-45	42	1
15	325	TP MIL 50	73-2	73	1
16	4813	26 III 303	21-8	42	1

## D Series of classification factors (contain other vigorous characters than those above mentioned)

Exptl. var. no.	Accession no.	Variety name	Seed source	Origin	Variety
D 1	1146	JU KU	92-5	20	1
2	818	MAGAGA	73-2	73	1
3	606	MAKAPILAY PUSA B	73-2	73	1
4	21	MAYANG SABATIL 8	57-1	57	1
5	540	MINAGRA 1	72-1	72	1
6	539	MINAGRA 2	72-1	72	1
7	756	S. BAKOD	73-2	73	1
8	1229	TA CHU	92-5	20	1
9	64	T 141	42-48	42	1
10	9810	T 141	21-8		1
11	8188	PACHEHAI PERUMAL	21-3	42	1
12	10759	CI 8308			
13	3647	BASMATI	92-5	42	1
14-1	256	BJI	86-3	86	1
14-2	3711	BJI	92-5	42	1
15*		DONABARU			
16*		SML-KAPURI			
17	87	CHIANUNG 242	21-7	21	2
18-1	5915	SIAM 29	42-47	57	1
18-2	5916	"	42-47	57	1
18-3	27	"	57-1	57	1
18-4	42	"	73-2		1
19	251	BELLE PATNA	92-7	92	1
20	154	M 302	17-1	17	1
21	155	H 4	17-1	17	1
22	159	H 501	17-1	17	1
23		YONESHIO		50	2
24		JINHENG		53	2
25	7962	FUJISAKA NO. 5	92-5	50	2
26	9925	IR 8	73-3	73	1
28	2512	TANGINBOSHU	92-5	50	2

\* Missing data due to non-viable seed and non-seed.

\*\* See the Seed Source and Origin in the original catalog (IRRI, 1970).

\*\*\* Variety code, 1; *Indica* type, 2; *Japonica* type, 3; *Javanica* type.

In the Experiment I, all varieties were grown in one growing period with an aim of grasping the range of variation of net assimilation rate. Dose of fertilizers ( $\text{N-P}_2\text{O}_5\text{-K}_2\text{O}$ : 2-2-2 g/pot) and method of planting (direct sowing at a rate of 80 seeds/pot) were different from that of the experiments of the previous section. Seedlings of every varieties were grown without replicate in a/2000 porcelain Wagner pots at Mylor house from 26 March, 1971 and transferred to the lawn after one days. By thinning them for 3 successive times, number of seedlings per pot was reduced to 24 by the time 5 days before the first sampling. Twelve seedlings were harvested for the first sampling on 12 April, 1971 when IR8 reached the 5th leaf age. Remaining 12 seedlings for the second sampling were harvested 9 days after. Four of 12 seedlings were used for leaf area measurement. In this experiment, results were obtained with 238 varieties. Other varieties used failed to grow due to non-viable and ungerminated seeds (due to imperfect breaking of dormancy).

In the Experiment II, 227 varieties including ungerminated seeds in the Experiment I were examined with the randomized method with 3 replicates over 5 times from May to September, 1971. Clay pots with the size of 30 cm of upper diameter and 20 cm of bottom diameter containing 7 kg of soil were used, which painted coaltar on the inner surface. Fertilizers were applied at a rate of  $\text{N-P}_2\text{O}_5\text{-K}_2\text{O}$ ; 1.5-0.8-1.0/pot. Relatively uniform 10 seedlings were transplanted at the 2.5th to 3rd leaf age. Five plants were harvested at the 5th leaf age of an index plant, IR8, and remaining 5 plants were harvested 7 days after. Two of 5 plants were used for leaf area measurement. Other procedures were the same as in the Experiment I. Sometimes, Mypcin was applied for protecting brown plant hopper and green leaf hopper 4 days before the first sampling.

In the Experiment III, 47 varieties with higher or lower net assimilation rate identified in the Experiment II were examined. Twenty seedlings were transplanted to a Wagner porcelain pot of a/2000. Other experimental procedures were the same as in the Experiment II. Plants were grown for growth analysis from 20 to 27, December, 1971.

In the Experiment IV, 30 varieties among 47 used in the Experiment III were examined for growth measurement on 15-22, March, 1972. Other experimental procedures were the same as in the Experiment III.

## (2) Results and discussion

In the Experiment I, 238 varieties including an index variety, IR8, were grown in one condition without replicate and net assimilation rate and related functions were determined (41, 64). Net assimilation rate obtained from all varieties showed the mean value of  $96.5 \text{ mg dm}^{-2} \text{ hr}^{-1}$ , with standard deviation 20.3 and variation coefficient 21.1%. Relatively large differences among varieties were recognized. Figure 1 shows the frequency distribution of net assimilation rate of all varieties examined in the Experiment I. Net assimilation rate shows a normal distribution and that of IR8 is located at around middle point. Figure 2 shows the significant relationship between the net assimilation rate and relative growth rate ( $r=0.389^{**}$ ). Although it is not quite certain yet whether extremely high or low value of net assimilation rate is intrinsic characters of varieties or experimental error it can be recognized that there is a great possibility to search for varieties with higher net assimilation rate than that of present improved varieties.

In the Experiment II, 227 varieties including examined and not-examined varieties in the Experiment I were more carefully studied with 3 replicates. The experiment was repeated over 5 times (experimental series 1-5) during a period from May to September.

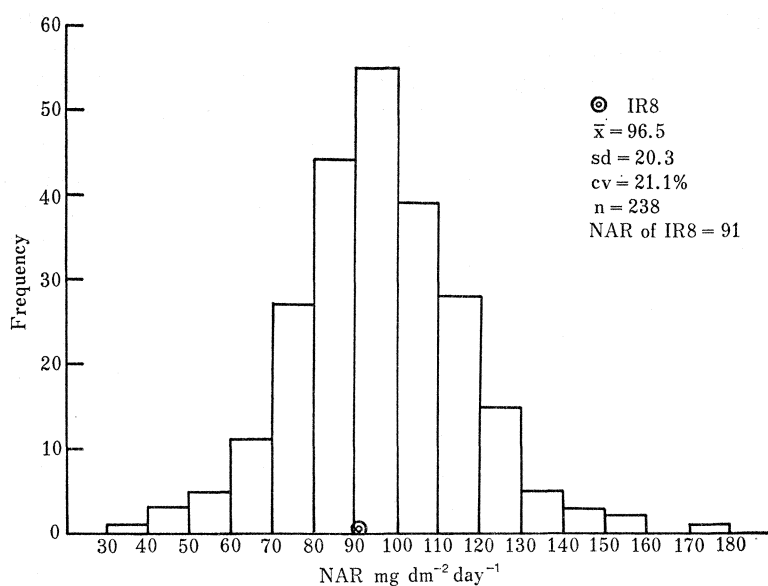


Fig. 1 Frequency distribution of net assimilation rate in Experiment I.

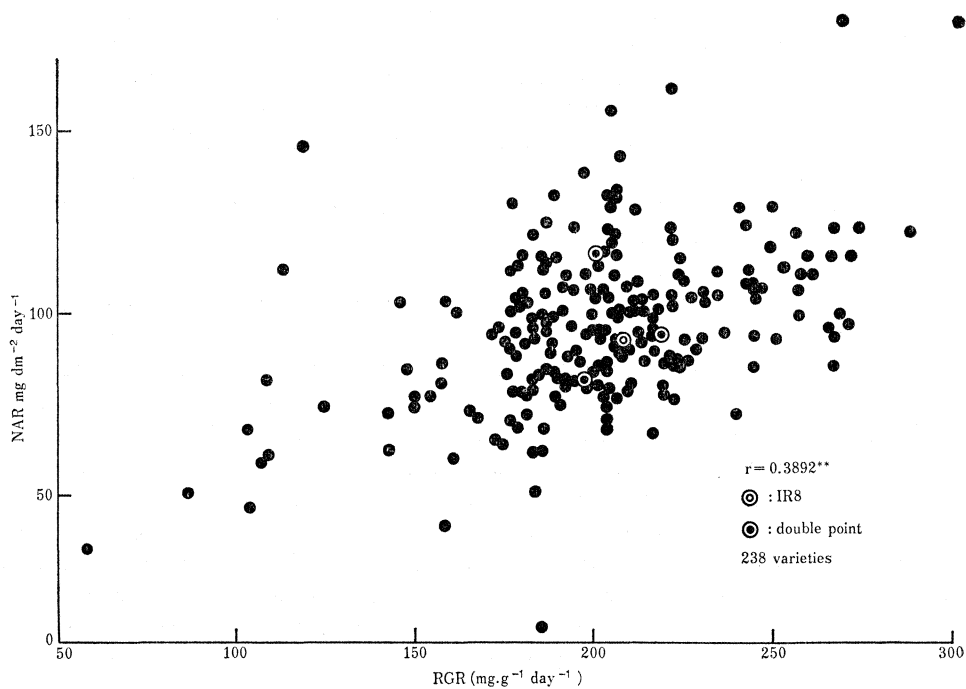


Fig. 2 Relationship between net assimilation rate and relative growth rate among different rice varieties (Experiment I).

Net assimilation rate obtained at each time was that influenced by different climatic conditions according to growing seasons. Figure 3 shows frequency distribution of NAR obtained at each experimental series. All of them can be regarded as showing normal distribution. NAR of IR8 was located slightly lower than the middle point in the frequency distribution of each experiment. This shows clearly that varieties with higher NAR than that of IR8 actually exist as already shown in the Experiment I. Table 6 a and b show net assimilation rate, relative growth rate and specific leaf weight (SLW) of each variety examined in the experimental series 1-5. Table 7 indicates that there are some varieties which have NAR higher than the lowest one by 44 to 82%, and higher than that of IR8 by 22 to 47% with 12% of coefficient of variability at the most.

In the Experiment III, 47 varieties which had shown NAR higher or lower by more than 20% than the average of 227 varieties examined in the Experiment II were studied, but, due to insect damage data were obtained with 32 varieties out of 47 varieties used. In Table 8, the mean NARs of varieties, calculated by variance analysis and Duncan's range test are given in a decreasing order. Variance analysis shows significant difference at 1% level between varieties but insignificant differences among replicates. Experiment III shows the result that there are varieties with higher NAR than that of IR8 as already recognized in the Experiment II. This experiment was performed under the condition of solar radiations of  $253 \text{ ly}^{-2} \text{ day}^{-1}$  and the mean temperature of  $25.3^\circ\text{C}$  at the end of rainy season.

It has been known that net assimilation rate is affected by climatic factors (28, 84). However if there is no large difference in correlation of NAR between experiments conducted under different climatic conditions, NAR determined at any season could be used for the comparison of varieties. From this point of view the Experiment IV was carried out under the climatic condition different from that of the Experiment III. Results of variance analysis and Duncan's range test shown in Table 9 indicate significant difference

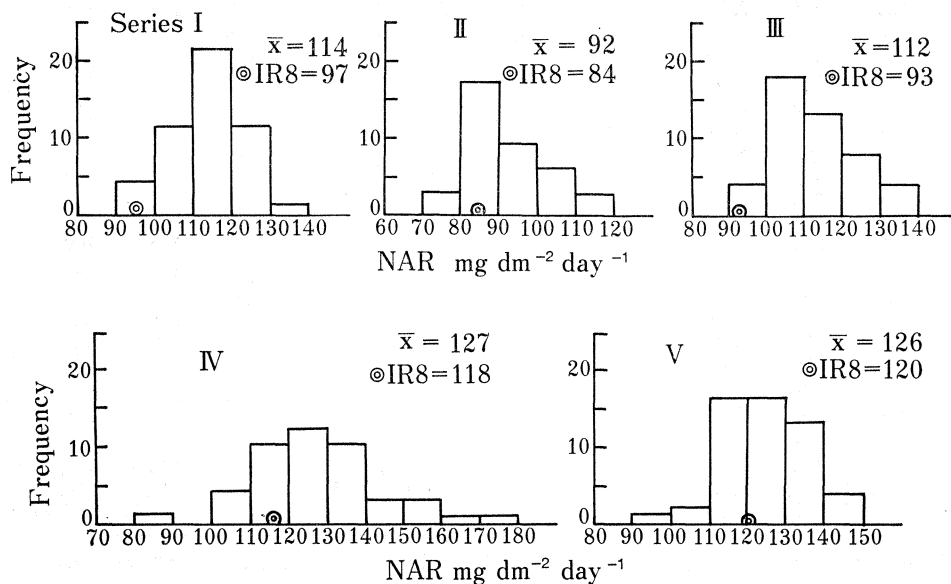


Fig. 3 Frequency distribution of net assimilation rate in each experimental series of Experiment II.

**Table 6a. List of net assimilation rate, relative growth rate and SLW<sub>2</sub> of rice varieties (Experiment II).**

Series 1 <sup>1)</sup>				Series 2 <sup>2)</sup>				Series 3 <sup>3)</sup>			
Exptl. var. no.	NAR mg dm <sup>-2</sup> day <sup>-1</sup>	RGR mg g <sup>-1</sup> day <sup>-1</sup>	SLW <sub>2</sub> mg cm <sup>-2</sup>	Exptl. var. no.	NAR mg dm <sup>-2</sup> day <sup>-1</sup>	RGR mg g <sup>-1</sup> day <sup>-1</sup>	SLW <sub>2</sub> mg cm <sup>-2</sup>	Exptl. var. no.	NAR mg dm <sup>-2</sup> day <sup>-1</sup>	RGR mg g <sup>-1</sup> day <sup>-1</sup>	SLW <sub>2</sub> mg cm <sup>-2</sup>
B-1	110	214	2.29	B-55	108	220	2.81	B-106	96	191	2.82
2	125	231	2.62	56	102	200	2.55	107	108	226	2.84
3	108	242	2.66	57	86	193	2.71	109	114	236	2.73
4	127	231	2.63	58	82	178	2.79	110	113	240	2.87
5	118	235	2.40	59	75	139	2.98	111	101	208	2.67
6	94	213	2.21	60	91	209	2.49	113	116	226	2.70
7	110	207	2.87	61	83	177	2.65	114	121	220	2.89
9	112	237	2.57	62	84	193	2.55	115	112	239	2.50
11	115	227	2.77	63	114	211	3.11	116	117	236	2.51
12	122	237	2.60	64	73	167	2.64	117	126	234	2.82
13	127	239	2.90	65	85	170	3.09	118	131	221	3.21
14	118	232	2.47	66	88	175	3.00	119	102	200	2.73
15	118	227	2.61	67	82	175	2.81	120	107	231	2.46
16	136	223	3.13	68	78	171	2.77	121	136	266	2.94
17	107	226	2.62	69	87	198	2.48	122	107	224	2.62
18	114	235	2.67	72	113	221	2.85	123	113	233	2.89
19	103	205	2.53	75	112	222	2.84	124	101	217	2.77
20	106	231	2.32	81	93	194	2.71	125	107	212	2.80
21	112	249	2.44	82	80	172	2.63	126	111	221	2.73
22	101	214	2.58	84	83	153	2.90	127	118	221	3.01
23	114	223	2.39	85	93	185	2.88	128	101	206	2.67
24	108	212	2.22	86	110	193	2.83	129	113	220	3.03
25	113	249	2.54	87	107	217	2.67	130	111	249	2.62
26	119	220	2.94	88	100	224	2.66	131	116	230	2.95
27	118	214	3.13	91	87	180	2.70	132	121	236	3.09
29	127	204	3.09	92	81	168	2.68	133	103	239	2.66
30	111	220	2.60	93	88	185	2.57	134	137	247	3.09
31	121	232	2.86	94	83	174	2.56	135	121	257	2.60
32	117	232	2.61	95	92	201	2.47	136	122	240	2.84
33	123	224	2.79	96	82	171	2.61	137	108	225	2.60
34	123	213	2.51	97	99	198	2.62	138	135	250	2.87
35	118	235	2.67	98	91	177	2.72	139	114	225	2.87
37	112	238	2.64	99	90	173	2.85	140	122	251	2.75
38	117	223	2.77	101	100	199	2.64	141	113	214	2.70
39	114	235	2.75	102	94	195	2.94	142	123	252	2.88
40	112	232	2.51	104	97	196	2.66	143	108	226	2.71
41	114	229	2.94	105	110	204	2.92	144	108	230	2.84
42	109	235	2.69	IR8	84	177	2.87	145	94	188	2.78
44	124	224	2.97					146	94	214	2.80
45	98	220	2.45					147	106	209	2.82
46	113	208	3.03					148	103	230	2.74
47	121	197	3.39					149	105	245	2.57
48	107	218	2.78					151	104	243	2.58
50	121	224	3.09					152	109	212	2.74
51	115	220	2.91					153	127	251	2.79
53	94	225	2.42					154	107	208	2.80
54	109	205	3.00					IR8	93	226	2.53
IR8	97	213	2.70								
$\bar{x}$	114.0	224.5	2.69		92.0	187.7	2.74		112.3	228.2	2.78
sd	8.86	11.9	0.263		11.2	19.9	0.165		10.7	16.9	0.162
cv%	7.77	5.31	9.78		12.7	10.6	1.02		9.53	7.44	5.83

1) Series 1 performed in triplicates from May 17 to 27, 1971 under 492 ly day<sup>-1</sup> of mean solar radiation and 30.0°C of mean temperature.

2) Series 2 from June 10 to 17, 1971 under 167 ly day<sup>-1</sup> and 25.9°C.

3) Series 3 from July 6 to 13, 1971 under 328 ly day<sup>-1</sup> and 27.4°C.

**Table 6b. List of net assimilation rate, relative growth rate and SLW<sub>2</sub> of rice varieties (Experiment II).**

Series 4 <sup>1)</sup>				Series 5 <sup>2)</sup>			
Exptl. var. no.	NAR mg dm <sup>-2</sup> day <sup>-1</sup>	RGR mg g <sup>-1</sup> day <sup>-1</sup>	SLW <sub>2</sub> mg cm <sup>-2</sup>	Exptl. var. no.	NAR mg dm <sup>-2</sup> day <sup>-1</sup>	RGR mg g <sup>-1</sup> day <sup>-1</sup>	SLW <sub>2</sub> mg cm <sup>-2</sup>
B-155	126	241	2.62	B-207	119	242	2.75
156	138	247	3.04	208	116	252	2.68
159	100	233	2.42	209	96	225	2.68
160	161	252	2.96	210	122	214	3.19
161	157	245	3.05	212	124	238	3.16
162	117	228	2.83	213	114	238	2.67
163	128	248	2.83	217	127	227	3.16
164	131	241	2.83	220	117	278	2.97
166	135	255	2.65	224	120	229	2.93
167	108	247	2.35	226	115	237	2.93
168	132	264	2.66	228	133	238	3.24
169	126	224	2.68	233	145	276	3.31
170	117	235	2.47	234	126	261	2.97
171	117	222	2.80	237	136	238	3.47
172	129	261	2.53	238	132	264	2.87
173	123	245	2.79	241	130	256	3.01
175	122	253	2.72	243	112	244	2.78
176	125	259	2.75	246	129	234	3.11
177	137	275	2.84	A-2	115	238	2.75
178	133	254	2.89	5	136	258	2.81
180	122	245	2.83	6	123	225	3.15
181	133	281	2.80	7	134	247	2.79
182	113	232	2.77	10	124	247	2.98
183	122	243	2.87	12	128	264	2.72
184	131	262	2.94	14	130	267	2.88
185	117	236	2.89	16	127	346	3.05
186	120	259	2.68	17	135	261	2.87
187	160	248	3.50	20	126	250	2.99
188	88	215	2.52	22	139	283	2.84
190	117	222	2.81	25	128	252	2.90
191	118	226	3.08	26	118	232	2.79
193	134	252	2.98	30	144	252	3.06
194	126	241	2.66	31	114	242	2.64
196	141	260	3.15	32	119	251	2.72
197	173	260	2.84	C-1	116	218	2.93
198	150	267	3.14	5	120	253	2.77
199	107	230	2.61	8	133	259	3.07
200	103	230	2.59	13	107	221	2.71
201	156	269	3.29	15	131	238	3.19
202	148	237	3.50	16	109	252	2.77
203	122	254	2.64	D-1	121	241	2.72
204	126	262	2.77	2	137	251	3.30
205	116	242	2.60	4	117	259	2.51
206	139	239	3.28	8	129	259	2.86
IR8	118	248	2.67	14-1	137	251	3.09
				14-2	130	246	2.91
				18-1	115	225	2.86
				18-2	133	245	3.01
				20	146	261	3.30
				21	140	250	3.01
				26	146	257	2.83
				IR8	120	239	2.84
$\bar{x}$	127.2	246.4	2.82		125.8	246.8	2.934
sd	15.3	14.9	0.255		10.7	15.1	0.202
cv%	12.03	6.06	9.04		8.51	6.11	6.90

1) Series 4 performed from Aug. 5 to 12 under 367 ly day<sup>-1</sup> and 27.5°C.

2) Series 5 performed from Sept. 5 to 12 under 389 ly day<sup>-1</sup> and 25.4°C.

**Table 7 Existence of varietal differences in net assimilation rate of rice plants.**

Experimental series in Expt. II	No. of varieties examined	NAR (mg dm <sup>-2</sup> day <sup>-1</sup> )				Variability			
		Max.	Min.	Ave.	IR 8	% of NAR max. over NAR min.	% of NAR max. over NAR <sub>IR8</sub>	sd	cv%
1	49	134.1	9.34	114.0	106.2	44	26	8.86	7.77
2	37	114.2	73.1	92.0	84.3	56	35	11.2	12.17
3	46	137.1	94.1	112.3	93.1	45	47	10.7	9.53
4	44	161.4	88.4	127.2	118.1	82	36	15.3	12.03
5	51	146.2	96.2	125.8	120.2	52	22	10.7	8.57

Series 1 performed in triplicate from May 17 to 27, 1971 under 492 ly day<sup>-1</sup> mean solar radiation and 30.0°C mean temperature.

Series 2 performed from June 10 to 17, 1971 under 167 ly day<sup>-1</sup> and 25.9°C.

Series 3 performed from July 6 to 13, 1971 under 328 ly day<sup>-1</sup> and 27.4°C.

Series 4 performed from Aug. 5 to 12, 1971 under 367 ly day<sup>-1</sup> and 27.5°C.

Series 5 performed from Sept. 5 to 12, 1971 under 339 ly day<sup>-1</sup> and 25.4°C.

at 1% level among NARs of varieties, although it shows relatively large variance among replicates. With 29 varieties commonly used in the Experiment III and IV, correlation coefficient was calculated. Table 10 shows significant correlation coefficient ( $r=0.639^{**}$ ) between NARs determined in 2 experiments.

Table 11 shows that there were significant differences among varieties, between experiments and variety-experiment interaction. In other words, net assimilation rate indicated significant varietal differences in both experiments which were carried out under different climatic conditions but the absolute values of the rate differed each other. The order of NAR among varieties also differed in both experiments as indicated by the significant variety-experiment interaction. However, it can be considered that these problems may not disturb so seriously the assessment of the varietal differences in NAR, because of the fact that there exists the heritability of NAR as shown below and that significant correlation coefficient between both experiments is shown.

According to Hayashi (29) net assimilation rate of rice varieties was affected with the change of solar radiation. The extent of the change differs with varieties. Apparently, a linear function between solar radiation and net assimilation rate was observed, of which regression coefficient was dependent upon variety. Besides, it was observed that the regression coefficient between net assimilation rate under the natural solar radiation and the attenuated solar radiation had a close positive relationship. This means that varieties showing higher NAR under higher radiation tend to express a larger extent of decrease of NAR under lower radiation. In the present experiment, net assimilation rate decreased by the decrease of solar radiation and temperature as shown in Table 10. Table 12 a and b show the analysis of variance of 29 varieties examined commonly in the Experiment III and Experiment IV.

Heritability for net assimilation rate of varieties is obtained from the equation as follows (29, 45);

**Table 8 Differences of NAR among selected rice varieties  
grown at wet season (Experiment III).**

Var. no.	NAR <sup>1)</sup> mg dm <sup>-2</sup> day <sup>-1</sup>	Range test <sup>2)</sup>
B—160	114.5	a
—187	112.1	a b
—134	109.6	b c
—56	107.5	c d
—202	103.9	d e
A—30	103.6	e
D—20	103.1	e
B—75	102.3	e
—88	100.5	e f
—116	98.3	f g
—138	98.0	f g
—63	95.5	g h
—161	94.8	g h i
—201	93.4	h i j
—198	93.3	h i j
—101	93.2	h i j
—114	92.3	h i j
—127	92.0	h i j
—140	91.4	i j k
T 141	90.7	j k l
B—64	88.0	k l m
—188	87.9	k l m
—16	87.2	l m n
—87	85.7	m n o
IR 8	83.7	o p
B—132	83.6	o p
—69	83.1	o p
—136	82.4	o p q
—142	81.7	p q r
—59	79.1	q r
—233	78.6	r
—213	74.0	s

Analysis of variance

Source	df	ss	ms	F
Total	97	12,594.66		
Varieties	31	10,189.89	328.71	9.55**
Block	2	202.51	101.26	2.94 <sup>ns</sup>
Error	64	2,202.26	34.41	

1) NAR measured from Dec. 20 to 27, 1971 under 253 ly day<sup>-1</sup> and m. t. 25.3°C.

2) Duncan's multiple range test at 5 % level.

\*\* Significant at 1 % level. ns: insignificant.



**Table 9 Differences of NAR among selected rice varieties grown at dry season (Experiment IV).**

Exptl. var. no.	NAR mg dm <sup>-2</sup> day <sup>-1</sup>	Range test <sup>2)</sup>
A— 30	128.7	a
B—202	128.7	a
— 84	124.3	a b
—118	122.7	b c
—113	120.3	b c d
—187	120.0	b c d
—134	119.5	c d
—114	119.3	c d
—160	118.7	c d
—116	117.3	d
—161	116.3	d
D— 20	115.7	d
B— 56	108.7	e
—121	108.5	e
—209	107.7	e f
—188	106.7	e f
— 59	106.0	e f
— 16	105.2	e f g
—136	104.5	e f g
— 75	103.2	f g h
—132	101.2	g h i
—117	101.0	g h i
—105	100.7	g h i
—140	99.4	h i j
— 64	98.4	i j k
— 88	98.0	i j k
—200	95.3	j k
T 141	94.4	k
B—201	94.4	k
IR 3	90.0	l

Analysis of variance

Source	df	ss	ms	F
Total	89	14,557.0		
Varieties	29	10,351.0	356.93	6.72**
Block	2	1,126.8	563.40	10.61**
Error	58	3,079.2	53.089	

1) NAR measured from March 15 to 22, 1972 under average solar radiation of 379 ly day<sup>-1</sup> and mean temperature of 29.0°C.

2) Duncan's multiple range test at 5 % level.

\*\* Significant at 1 % level.

**Table 10 Relationship between NAR in Experiment III and IV under different climatic conditions.**

Exptl. Var. no.	Expt. IV <sup>1)</sup>	Expt. III <sup>2)</sup>
B— 16	105	87
— 56	109	108
— 75	103	102
— 84	124	106
— 88	98	101
—105	101	88
—113	120	103
—114	119	92
—116	111	98
—117	101	104
—118	123	104
—121	120	100
—132	101	84
—134	114	110
—136	104	82
—140	99	91
—160	119	115
—161	116	95
—187	120	112
—201	95	93
—202	129	104
A— 30	129	104
D— 20	116	103
B— 59	106	79
— 64	99	88
—188	107	88
—200	95	84
T 141	94	91
IR 8	92	84
x	109.6	96.4
sd	11.0	10.9
cv %	10.0	10.9

Correlation coefficient between Experiment IV and III  $r=0.639^{**}$

- 1) Expt. IV performed from March 15 to 22, 1972 under average solar radiation of  $379 \text{ ly day}^{-1}$  and mean temperature of  $29.0^{\circ}\text{C}$ .
- 2) Expt. III performed from December 20 to 27, 1971 under average solar radiation of  $253 \text{ ly day}^{-1}$  and mean temperature of  $25.3^{\circ}\text{C}$ .

**Table 11 Analysis of variance on NAR between Experiment III and IV.**

Source	df	ss	ms	F
Total	173	33,820.23		
Varieties	28	14,529.21	518.90	9.11**
Experiment	1	4,544.83	4,544.83	79.82**
Var. x Expt.	28	7,002.17	250.08	4.39**
Error	136	7,744.02	56.94	

**Table 12a. Analysis of variance on NAR of varieties in Experiment III.**

Source	df	ss	ms	F
Total	86	11,905.81		
Varieties	28	8,053.68	287.63	4.23**
Block	2	52.16	26.08	0.38 <sup>ns</sup>
Error	56	3,799.97	67.86	

**Table 12b. Analysis of variance on NAR of the same varieties as used in Experiment III in Experiment IV.**

Source	df	ss	ms	F
Total	86	13,912.27		
Varieties	28	10,020.23	357.87	7.01**
Block	2	1,035.20	517.60	10.15**
Error	56	2,856.84	51.02	

$$\begin{aligned}
 \text{Heritability} &= \frac{\text{genotype variance}}{\text{phenotype variance}} \\
 &= \frac{\text{genotype variance}}{\text{genotype variance} + \text{environmental variance}} \\
 &= \frac{(MS_1 - MS_2) / r}{(MS_1 - MS_2) / r + MS_2 / r} = \frac{MS_1 - MS_2}{MS_1}
 \end{aligned}$$

$MS_1$  = Variance of varieties

$MS_2$  = Variance of error

$r$  = number of replicate

If heritability of varieties is obtained from the mean of square in Table 12, heritability of NAR of varieties is 76% in the Experiment III and 86% in Experiment IV. Since both experiments were performed in the rainy season or dry season respectively, it can be considered that almost the similar heritability can be obtained even if NAR is measured at any season in the tropics. Therefore, selection of higher photosynthetic varieties may possibly be made by measuring net assimilation rate as a photosynthetic capacity.

From the above experimental results, it is recognized that there are relatively large differences of NAR, which can be taken as an index of photosynthetic capacity, among varieties of *Indica* rice. The fact that the improved variety, IR8, has the approximately middle value of NAR among varieties examined indicates that there are many other varieties having NAR higher than IR8. The results show also that the ranking of NAR

among varieties is relatively stable, although the absolute value of NAR of varieties fluctuates depending on changes of climatic environment especially of solar radiation. Since it was shown that heritability of NAR of rice varieties was approximately equivalent even when the varieties were grown either in the wet season or in the dry season of the tropics, selection of varieties or lines for higher photosynthetic capacity may be possible based on the measurement of net assimilation rate carried out at any season.

### 3. Plant characters relating to net assimilation rate

In the previous section, it was clearly recognized that there were distinct varietal differences of net assimilation rate in *Indica* rice. It is presumed that some morphological characters of rice may relate to net assimilation rate. The relationship between net assimilation rate and morphological characters of rice was investigated in this section.

#### (1) Materials and methods

In multiple regression analysis, NAR and morphological characters of 32 varieties and other varieties examined in the Experiment III, which had 2 replicates, were used. Leaf area, leaf weight, number of stem, total dry weight, plant height and number of leaf were measured at the first and the second sampling during growing period in the Experiment III. Data in Experiment II, Experiment III and Experiment IV were used for calculating dry weight per unit leaf area and leaf nitrogen content. Nitrogen was analyzed by the semi-micro Kjeldahl method. Multiple regression analysis was made by stepwise regression procedure coded by Kawabata (38) with HITAC 8000 at Computing Center of Agriculture, Forestry and Fisheries Research Council of the Ministry of Agriculture and Forestry of Japan.

#### (2) Results and discussion

The following morphological characters were determined at the growth stage when NAR was measured in the Experiment III. Dry weight per unit leaf area ( $SLW_1$ ,  $SLW_2$  mg/cm<sup>2</sup>), leaf area ( $LA_1$ ,  $LA_2$  cm<sup>2</sup>/plant), number of leaves ( $L_1$ ,  $L_2$  number/plant), number of stems ( $T_1$ ,  $T_2$  number/hill), total dry weight ( $W_1$ ,  $W_2$  g/plant), plant height ( $H_1$ ,  $H_2$  cm), leaf area increase ( $\Delta LA$  cm<sup>2</sup>/plant), tiller increase ( $\Delta T$  number/hill), increased number of leaves ( $\Delta L$  number/hill), plant height increase ( $\Delta H$  cm),  $\Delta L/\Delta T$ ,  $\Delta W/\Delta T$ ,  $W_1/T_1$ ,  $W_2/T_2$ , leaf area per leaf blade ( $LA_1$ /leaf,  $LA_2$ /leaf, cm<sup>2</sup>/leaf) and number of days required for maturity (34) were measured. Table 13a and b show the correlation matrix of relationship among these 25 plant characters. The correlation coefficient in the following plant characters was similar in behavior;  $SLW$ , leaf area, number of leaf, total dry weight, plant height, dry weight per tiller and leaf area per leaf. On the contrary, there was no significant relationship between number of days for maturity and another characters except  $L_1$ . Table 13 also shows that there was significantly positive correlation between NAR and the following characters;  $SLW_1$ ,  $SLW_2$ ,  $H_1$ ,  $H_2$ ,  $\Delta L/\Delta T$ , and  $\Delta W/\Delta T$ . On the other hand, it shows that there was significantly negative correlation between NAR and the following characters;  $LA_1$ ,  $\Delta T$  and  $LA_1$ /leaf. It was recognized that NAR correlated most strongly to  $SLW_2$  among other characters.

Accordingly, multiple regression equation which was composed of NAR as a dependent variables was computed as shown in Table 14. In the equation,  $X_3$ ,  $X_{12}$ ,  $X_{14}$ ,  $X_{16}$  and  $X_{22}$ ,  $X_{21}$  shows  $SLW_2$ ,  $H_1$ ,  $\Delta LA$ ,  $\Delta L$ ,  $W_2/T_2$  and  $LA_1$ /leaf respectively. The equation indicated that overall F value and partial F value were significant and that determination coefficient  $R^2$  was 81.2%. Contribution of independent variables to  $\hat{Y}$  which was computed

Table 13a. Correlation matrix of 25 plant characters in Experiment III.

Entry	X <sub>1</sub>	X <sub>2</sub>	X <sub>3</sub>	X <sub>4</sub>	X <sub>5</sub>	X <sub>6</sub>	X <sub>7</sub>	X <sub>8</sub>	X <sub>9</sub>	X <sub>10</sub>	X <sub>11</sub>	X <sub>12</sub>	X <sub>13</sub>
Maturity X <sub>1</sub>	—	-.073	-.151	.003	.124	.374**	.268	.247	.211	.013	.101	.069	.086
SLW <sub>1</sub> X <sub>2</sub>	-.073	—	.760**	-.533**	-.437**	-.054	.015	.039	-.065	-.179	-.196	.205	.152
SLW <sub>2</sub> X <sub>3</sub>	-.151	.760**	—	-.186	-.269	-.199	-.152	-.086	-.199	.131	.133	.518**	.520**
LA <sub>1</sub> X <sub>4</sub>	.003	-.533**	-.186	—	.885**	.162	.115	.214	.223	.906**	.854**	.373**	.367*
LA <sub>2</sub> X <sub>5</sub>	.124	-.437**	-.269	.885**	—	.424**	.409**	.437**	.429**	.809**	.878**	.298*	.265
L <sub>1</sub> X <sub>6</sub>	.374**	-.054	-.199	.162	.424**	—	.851**	.861**	.807**	.150	.332*	-.143	-.144
L <sub>2</sub> X <sub>7</sub>	.268	.015	-.152	.115	.409**	.851**	—	.803**	.871**	.101	.287*	-.237	-.238
T <sub>1</sub> X <sub>8</sub>	.247	.039	-.086	.214	.437**	.861**	.803**	—	.839**	.258	.392**	-.018	-.129
T <sub>2</sub> X <sub>9</sub>	.211	-.065	-.199	.223	.429**	.807**	.871**	.839**	—	.190	.275	-.216	-.268
W <sub>1</sub> X <sub>10</sub>	.013	-.179	.131	.906**	.809**	.150	.101	.258	.190	—	.914**	.587**	.543**
W <sub>2</sub> X <sub>11</sub>	.101	-.196	.133	.853**	.878**	.332*	.287*	.392**	.275	.914**	—	.592**	.569**
H <sub>1</sub> X <sub>12</sub>	.069	.205	.518**	.373**	.298*	-.143	-.237	-.081	-.216	.587**	.592**	—	.926**
H <sub>2</sub> X <sub>13</sub>	.086	.152	.520**	.367**	.265	-.144	-.238	-.129	-.268	.543**	.659**	.926**	—
$\Delta$ LA X <sub>14</sub>	.147	-.358*	-.268	.779**	.978**	.484**	.483**	.482**	.460**	.714**	.835**	.281	.225
$\Delta$ T X <sub>15</sub>	.052	-.170	-.245	.118	.193	.311*	.505**	.184	.690**	-.000	-.024	-.282*	-.311*
$\Delta$ L X <sub>16</sub>	.118	.061	-.086	.068	.313*	.534**	.895**	.572**	.732**	.052	.194	-.258	-.254
$\Delta$ W X <sub>17</sub>	.119	-.193	.128	.808**	.872**	.370*	.332*	.418**	.293*	.857**	.990**	.569**	.552**
$\Delta$ H X <sub>18</sub>	.087	-.022	.294*	.206	.094	-.070	-.121	-.150	-.238	.228	.285*	.375**	.696**
$\Delta$ L/ $\Delta$ T X <sub>19</sub>	.024	.162	.071	-.128	.055	.193	.358*	.317*	.016	-.087	.094	-.047	.039
$\Delta$ W/ $\Delta$ T X <sub>20</sub>	-.021	.059	.287*	.319*	.343*	.035	-.095	.145	-.302*	.453**	.572**	.526**	.551**
W <sub>1</sub> /T <sub>1</sub> X <sub>21</sub>	-.212	-.140	.195	.365*	.095	-.691**	-.664**	-.760**	-.623**	.382**	.219	.519**	.522**
W <sub>2</sub> /T <sub>2</sub> X <sub>22</sub>	-.073	-.103	.307*	.529**	.375*	-.330*	-.428**	-.314*	-.541**	.605**	.625**	.748**	.765**
LA <sub>2</sub> /1 X <sub>23</sub>	-.132	-.430**	-.101	.751**	.621**	-.291*	-.440*	-.232	-.302*	.691**	.613**	.537**	.486**
LA <sub>1</sub> /1 X <sub>24</sub>	-.269	-.437**	-.032	.754**	.475**	-.491**	-.443**	-.381**	-.313*	.679**	.510**	.460**	.437**
NAR X <sub>25</sub>	.111	.600**	.717**	-.301*	-.219	.085	.071	.117	-.086	-.046	.156	.489**	.487**

\* Significant at 5 % level.

\*\* Significant at 1 % level.

**Table 13b. Correlation matrix of 25 plant characters in Experiment III (continued).**

Entry		X <sub>14</sub>	X <sub>15</sub>	X <sub>16</sub>	X <sub>17</sub>	X <sub>18</sub>	X <sub>19</sub>	X <sub>20</sub>	X <sub>21</sub>	X <sub>22</sub>	X <sub>23</sub>	X <sub>24</sub>	X <sub>25</sub>
Maturity	X <sub>1</sub>	.147	.052	.118	.119	.087	.024	-.021	-.212	-.073	-.132	-.269	.111
SLW <sub>1</sub>	X <sub>2</sub>	-.358*	-.170	.061	-.193	-.022	.162	.059	-.140	-.103	-.430**	-.437**	.600**
SLW <sub>2</sub>	X <sub>3</sub>	-.268	-.245	-.086	.128	.294*	.071	.287*	.195	.307*	-.101	-.032	.717**
LA <sub>1</sub>	X <sub>4</sub>	.779**	.118	.068	.808**	.203	-.128	.319*	.365*	.529**	.751**	.754**	-.301*
LA <sub>2</sub>	X <sub>5</sub>	.978**	.193	.313*	.872**	.094	.055	.343*	.095	.375*	.621**	.475**	-.219
L <sub>1</sub>	X <sub>6</sub>	.484**	.311*	.534**	.370*	-.070	.193	.035	-.691**	-.330*	-.292*	-.491**	.085
L <sub>2</sub>	X <sub>7</sub>	.483**	.505**	.895**	.332*	-.121	.358*	-.095	-.664**	-.428**	-.440**	-.443**	.071
T <sub>1</sub>	X <sub>8</sub>	.482**	.184	.572**	.418**	-.150	.317*	.145	-.760**	-.314*	-.232	-.381**	.117
T <sub>2</sub>	X <sub>9</sub>	.460**	.690**	.732**	.293*	-.238	.016	-.302*	-.623**	-.541**	-.302*	-.313*	-.086
W <sub>1</sub>	X <sub>10</sub>	.714**	-.000	.052	.857**	.228	-.087	.453**	.382**	.605**	.691**	.679**	-.046
W <sub>2</sub>	X <sub>11</sub>	.835**	-.024	.194	.990**	.285	.094	.572**	.219	.625**	.613**	.510**	.156
H <sub>1</sub>	X <sub>12</sub>	.281	-.282*	-.258	.569**	.375**	-.047	.526**	.519**	.748**	.537**	.460**	.489**
H <sub>2</sub>	X <sub>13</sub>	.225	-.311*	-.254	.552**	.696**	.039	.551**	.522**	.765**	.486**	.437**	.487**
$\Delta LA$	X <sub>14</sub>	—	.189	.377**	.848**	.029	.130	.350*	-.001	.320*	.542**	.346*	-.158
$\Delta T$	X <sub>15</sub>	.189	—	.560**	-.027	-.231	-.392**	-.739**	-.115	-.558**	-.237	-.059	-.312*
$\Delta L$	X <sub>16</sub>	.377**	.560**	—	.230	-.122	.413**	-.186	-.478**	-.407**	-.456**	-.283	.036
$\Delta W$	X <sub>17</sub>	.848**	-.027	.230	—	.286	.143	.587**	.163	.606**	.573**	.442**	.213
$\Delta H$	X <sub>18</sub>	.029	-.231	-.122	.286	—	.200	.367*	-.288*	.461**	.172	.203	.263
$\Delta L/\Delta L$	X <sub>19</sub>	.130	-.392**	.413**	.143	.200	—	.531**	-.384**	.069	-.257	-.262	.286
$\Delta W/\Delta T$	X <sub>20</sub>	.350*	-.739**	-.186	.587**	.367*	.531**	—	.122	.749**	.429**	.222	.407**
W <sub>1</sub> /T <sub>1</sub>	X <sub>21</sub>	-.001	-.115	-.478**	.163	.288*	-.384**	.122	—	.687**	.656**	.800**	-.090
W <sub>2</sub> /T <sub>2</sub>	X <sub>22</sub>	.320*	-.558**	-.407**	.606**	.461**	.069	.749**	.687**	—	.734**	.668**	.277
LA <sub>2</sub> /1	X <sub>23</sub>	.542**	-.237	-.456**	.573**	.172	-.257	.429**	.646**	.734**	—	.833**	-.230
LA <sub>1</sub> /1	X <sub>24</sub>	.346*	-.059	-.283	.442**	.203	-.262	.222	.800**	.668**	.833**	—	-.316*
NAR	X <sub>25</sub>	-.158	-.312*	.036	.213	.263	.286	.407**	-.090	.277	-.230	-.316*	—

**Table 14 Multiple regression analysis of 25 plant characters against net assimilation rate by stepwise regression procedure\*.**

$$\hat{Y} = 26.904 + 15.891X_3 + 0.755X_{12} - 0.138X_{14} + 1.199X_{16} + 0.156X_{22} - 5.484X_{24}^{1)}$$

$$R^2 = 0.8116$$

Analysis of variance

Source	df	ss	ms	Overall F
Total	46	4,532.77		
Regression	6	3,679.01	613.17	28.72
Residual	40	873.77	21.34	

Coefficients and partial F, etc.

Var. no.	Mean	Stan. coeff. B	Partial coeff. B	Stand. error B	Partial F
X <sub>3</sub> SLW <sub>2</sub>	2.57	0.2969	15.891	5.661	7.89
X <sub>12</sub> H <sub>1</sub>	37.29	0.3731	0.755	0.253	8.91
X <sub>14</sub> ΔLA	76.20	-0.2198	-0.138	0.071	3.76
X <sub>16</sub> ΔL	5.69	0.2679	1.990	0.761	6.84
X <sub>22</sub> W <sub>2</sub> /T <sub>2</sub>	145.65	0.5500	0.156	0.039	15.98
X <sub>24</sub> LA <sub>1</sub> /leaf	4.74	-0.6940	-5.484	0.778	49.74

Constant term in regression equation = 26.904

Contribution of independent variables to  $\hat{Y}$

X <sub>3</sub>	12.36%
X <sub>12</sub>	15.53
X <sub>14</sub>	9.16
X <sub>16</sub>	11.16
X <sub>22</sub>	22.90
X <sub>24</sub>	28.90

- 1) X<sub>3</sub>: SLW at the 2nd sampling (SLW<sub>2</sub>, mg/cm<sup>2</sup>), X<sub>12</sub>: plant at the 1st sampling (H<sub>1</sub>, cm), X<sub>14</sub>: leaf area increase (ΔLA cm<sup>2</sup>/plt/week), X<sub>16</sub>: increase of leaf no. (ΔL, no./plt.), X<sub>22</sub>: total dry weight/tiller no. at the 2nd sampling (W<sub>2</sub>/T<sub>2</sub>), X<sub>24</sub>: leaf area/leaf at the 1st sampling (LA<sub>1</sub>/leaf, cm<sup>2</sup>/leaf)

\* Multiple regression analysis by stepwise regression procedure coded by K. Kawabata with HITAC 8000 in the Computing Center of the Agriculture, Forestry and Fisheries Research Council, Ministry of Agriculture and Forestry, Japan.

by partial regression coefficient indicated that X<sub>3</sub> (SLW<sub>2</sub>), X<sub>12</sub> (H<sub>1</sub>), X<sub>14</sub> (ΔLA), X<sub>16</sub> (ΔL), X<sub>22</sub> (W<sub>2</sub>/T<sub>2</sub>) and X<sub>24</sub> (LA<sub>1</sub>/leaf) were 12.4, 15.5, 9.2, 11.2, 22.9 and 28.9%, respectively. This means that the six characters mentioned above are important determinant factors of NAR. Thus, net assimilation rate can be forecasted with a probability of 81.2% by these characters. This procedure, however, does not have the practical usefulness in the forecast of NAR because more laborious works than direct measurement of NAR are required. On the other hand, this analysis is important in identifying major characters contributing to NAR and the extent of their contribution.

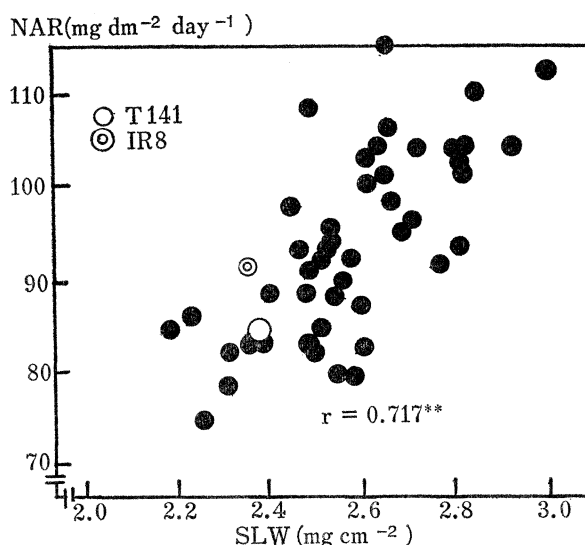


Fig. 4 Relationship between net assimilation rate and specific leaf weight among rice varieties (Experiment III, Dec. 1971).

The largest single correlation coefficient to NAR was that of  $\text{SLW}_2$  as shown in Table 13. Fig 4 shows the relation between NAR and SLW. Single regression equation between NAR and  $\text{SLW}_2$  which was obtained in the course of formulating multiple regression equation computed by stepwise regression procedure was indicated as follows;

$$Y = -5.32 + 38.39 X_3 \quad R^2 = 0.515$$

$$Y = \text{NAR}$$

$$X_3 = \text{SLW}_2$$

The regression explains that the relationship between NAR and  $\text{SLW}_2$  is 51.5%. Thus,  $\text{SLW}_2$  can be regarded as a useful primary index of selection for higher NAR varieties, if it is a stable character not being influenced by the change of environmental condition. Then, the stability of  $\text{SLW}$  to climatic conditions was examined.

Table 15 shows the significant correlationship at 1% level between NAR and  $\text{SLW}_2$  in the Experiment II, Experiment III and Experiment IV. Although the Experiment II was composed of 5 different experimental series which were performed from May to September, 1971, it was found consistently that NAR related closely to  $\text{SLW}_2$ . Table 16 shows that there were significant differences of  $\text{SLW}_2$  among varieties but there were neither significant difference between experiments nor interaction of varieties—experiment through both experiments. This means that absolute value of  $\text{SLW}_2$  obtained at the rainy season in the Experiment III did not differ from that at the dry season in the Experiment IV and that the order of  $\text{SLW}_2$  of varieties did not change significantly in both seasons. The leaf age of varieties used in both experiments was almost equivalent. Table 17 shows  $\text{SLW}_1$ ,  $\text{SLW}_2$  and the correlation coefficient between them in each experiment. Significant coefficients were indicated except a case. All these results indicate clearly that specific leaf weight of rice varieties is an extremely stable character against climatic conditions.

The specific leaf weight expresses the amount of dry matter per unit leaf area and does not necessary imply morphological thickness of leaf. In wheat, however a close



**Table 15 Relationship between NAR and SLW<sub>2</sub> in three experiments.**

Varieties	Expt. IV <sup>1)</sup>		Expt. III <sup>2)</sup>		Expt. II <sup>3)</sup>	
	NAR mg dm <sup>-2</sup> day <sup>-1</sup>	SLW <sub>2</sub> <sup>4)</sup> mg cm <sup>-2</sup>	NAR mg dm <sup>-2</sup> day <sup>-1</sup>	SLW <sub>2</sub> mg cm <sup>-2</sup>	NAR mg dm <sup>-2</sup> day <sup>-1</sup>	SLW <sub>2</sub> mg cm <sup>-2</sup>
B- 16	105	2.70	87	2.59	136	3.13
- 56	109	2.49	108	2.49	102	2.55
- 75	103	2.99	102	2.72	112	2.84
- 84	124	2.88	101	2.66	83	2.90
- 88	98	2.66	106	2.65	100	2.66
-105	101	2.41	88	2.55	110	2.92
-113	120	2.74	103	2.62	116	2.70
-114	119	2.56	92	2.58	121	2.89
-116	111	2.65	98	2.45	117	2.51
-117	101	2.27	104	2.63	126	2.82
-118	123	2.76	104	2.72	131	3.21
-121	120	2.57	100	2.62	136	2.94
-132	101	2.60	84	2.51	121	3.09
-134	114	2.78	110	2.86	137	2.55
-136	104	2.59	82	2.49	122	2.84
-140	99	2.32	91	2.49	122	2.75
-160	119	2.55	115	2.68	161	2.96
-161	116	2.70	95	2.69	158	3.05
-187	120	2.85	112	3.01	160	3.50
-201	95	2.86	93	2.82	156	3.29
-202	129	3.16	104	2.93	148	3.50
A- 30	129	3.03	104	2.82	144	2.82
D- 20	116	2.91	103	2.72	140	3.30
B- 59	106	2.67	79	2.58	75	2.98
- 64	99	2.40	88	2.48	73	2.64
-188	95	2.35	88	2.41	88	2.52
-200	101	2.24	84	2.31	103	2.59
-209	92	2.51	78	2.31	96	2.68
IR 8	94	2.47	84	2.38		

Correlation coefficient between NAR and SLW<sub>2</sub>

Experiment IV      r=0.6441\*\*

Experiment III      r=0.6996\*\*

Experiment II      r=0.5994\*\*

- 1) Experiment IV performed from March 15 to 22, 1972.
- 2) Experiment III performed from December 20 to 27, 1971.
- 3) Experiment II composed of 5 different experimental series which were performed from May to September, 1971.
- 4) Specific leaf weight measured at the second sampling.

**Table 16 Analysis of variance on  $SLW_2$  between Experiment III and IV.**

Source	df	ss	ms	F
Total	173	10.0564		
Varieties	28	6.4012	0.22861	9.79**
Experiment	1	0.0757	0.0757	3.24 <sup>ns</sup>
Var. x Expt.	28	0.8717	0.03113	1.34 <sup>ns</sup>
Error	116	2.7078	0.02334	

relationship between SLW and morphological thickness of leaf was reported (23). The amount of matters per unit leaf area may concurrently indicate the content of total nitrogen or protein nitrogen per unit leaf area. Figure 5 shows a close relationship between SLW and total nitrogen per unit leaf area in the Experiment III ( $r=0.954^{**}$ ). Figure 6 also shows the same relation. The larger is SLW, the larger the content of total nitrogen is. Consequently, there are close relationships between NAR and total nitrogen content per unit leaf area as shown in Fig. 7 and 8.

Table 18 shows the mean total nitrogen per unit leaf area of varieties used in the Experiment III and Experiment IV and the significant correlation coefficient ( $r=0.695^{**}$ ) between both experiments. Furthermore, Table 19 indicates the analysis of variance on total nitrogen between both experiments, which shows significant differences among varieties and between experiments but not significant interaction between varieties and experiments. Namely, it is aparent that there are varietal differences in total nitrogen content per unit leaf area and the relative order of it among varieties does not change due to different climatic condition. Therefore, total nitrogen content per unit leaf area is also regarded as a stable character as SLW as far as the inorganic nutrition of plants is not restricted. Total nitrogen content per unit leaf area as well as specific leaf weight can be used as a criterion in selecting higher NAR varieties.

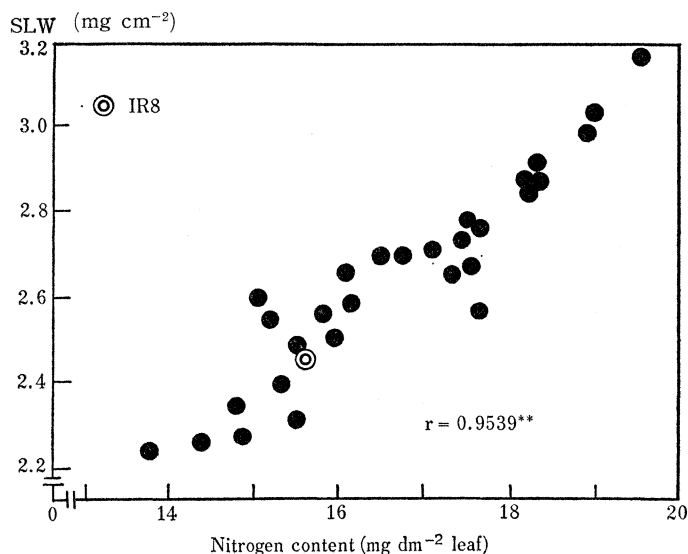


Fig. 5 Relationship between specific leaf weight and nitrogen content per unit leaf area among rice varieties (Experiment III, Dec. 1971).

**Table 17 Relationship of SLW between experiments.**

Exptl. var. no.	SLW <sub>1</sub> <sup>1)</sup>		SLW <sub>2</sub> <sup>2)</sup>		
	Expt. III <sup>3)</sup>	Expt. IV <sup>4)</sup>	Expt. II <sup>5)</sup>	Expt. III	Expt. IV
B- 16	2.40	2.32	3.13	2.59	2.70
- 56	2.05	2.22	2.55	2.49	2.49
- 75	2.53	2.58	2.84	2.72	2.99
- 84	2.76	2.56	2.90	2.66	2.88
- 88	2.61	2.26	2.66	2.65	2.66
-105	2.49	2.49	2.92	2.55	2.41
-113	2.69	2.58	2.70	2.62	2.74
-114	2.62	2.54	2.89	2.58	2.56
-116	2.38	2.54	2.51	2.45	2.65
-117	2.62	2.18	2.82	2.63	2.27
-118	2.87	2.65	3.21	2.72	2.76
-121	2.61	2.41	2.94	2.62	2.57
-132	2.56	2.13	3.09	2.51	2.60
-134	2.78	2.40	2.55	2.86	2.78
-136	2.34	2.23	2.84	2.49	2.59
-140	2.46	2.26	2.75	2.49	2.32
-160	2.71	2.34	2.96	2.68	2.55
-161	2.57	2.70	3.05	2.69	2.70
-187	3.27	2.39	3.50	3.01	2.85
-201	2.85	2.44	3.29	2.82	2.86
-202	3.00	2.89	3.50	2.93	2.16
A- 30	2.76	2.48	2.82	2.82	3.03
D- 20	2.52	2.38	3.30	2.72	2.91
B- 59	2.34	2.60	2.98	2.58	2.67
- 64	2.26	2.12	2.64	2.48	2.40
-188	2.42	2.30	2.52	2.41	2.35
-200	2.09	2.11	2.59	2.31	2.24
-209	2.50	2.48	2.68	2.31	2.51
IR 8	2.37	2.47	2.69	2.38	2.47
$\bar{x}$	2.57	2.42	2.89	2.61	2.65
sd	0.258	0.188	0.280	0.173	0.229
cv%	10.0	7.78	9.67	6.63	8.62

## Correlation of SLW between experiments

	Expt. IV SLW <sub>1</sub>	Expt. II SLW <sub>2</sub>	Expt. III SLW <sub>2</sub>	Expt. IV SLW <sub>2</sub>
Expt. III SLW <sub>1</sub>	.473**	.652**	.837**	.372*
Expt. IV SLW <sub>1</sub>	—	.389*	.470**	.263
Expt. II SLW <sub>2</sub>		—	.669**	.545**
Expt. III SLW <sub>2</sub>			—	.752**

1) Specific leaf weight at the beginning of the growth analysis experiment.

2) Specific leaf weight at the end of the growth analysis experiment.

3) Experiment III performed from Dec. 20 to 27, 1971.

4) Expt. IV performed from March 15 to 22, 1972.

5) Expt. II composed of 5 different experimental series from May to September, 1971.

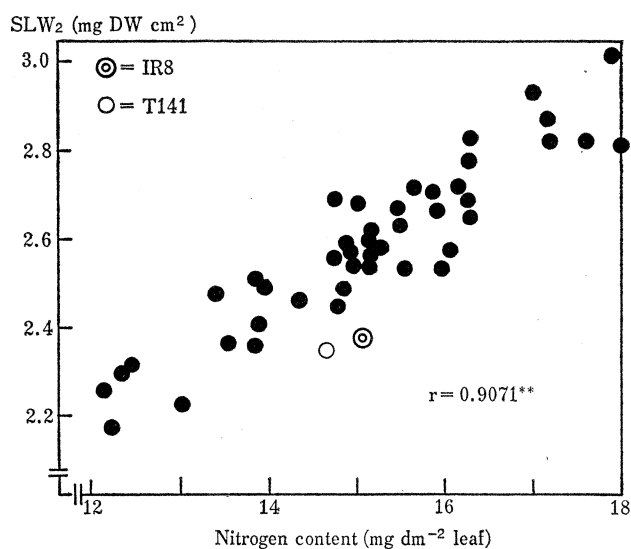


Fig. 6 Relationship between specific leaf weight and nitrogen content per unit leaf area among rice varieties (Experiment IV, March, 1972).

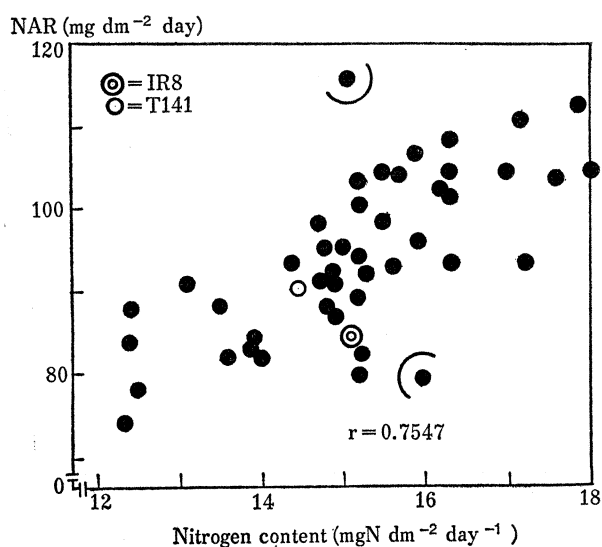


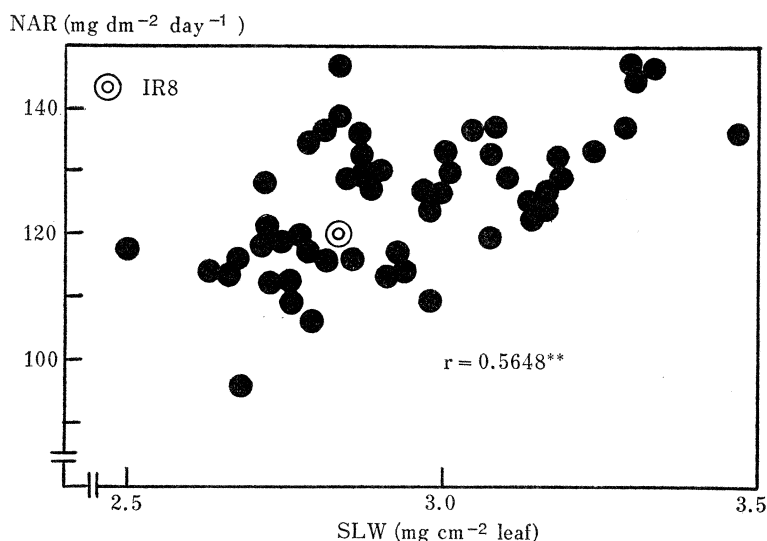
Fig. 7 Relationship between net assimilation rate and leaf nitrogen content per unit leaf area among rice varieties (Experiment III, Dec. 1971).

**Table 18 Relationship of nitrogen content per unit leaf area between Experiment III and IV.**

Exptl. var. no.	N mg dm <sup>-2</sup> leaves	
	Expt. III <sup>1)</sup>	Expt. IV <sup>2)</sup>
B- 16	14.9	16.7
- 56	16.3	15.5
- 59	16.1	16.5
- 64	13.5	15.3
- 75	16.2	18.9
- 84	15.9	18.3
- 88	16.3	16.1
-105	14.8	17.1
-113	15.2	17.4
-114	15.3	15.8
-116	14.7	17.3
-117	15.5	14.4
-118	15.7	17.6
-121	15.2	16.7
-132	13.9	15.0
-134	17.2	17.5
-136	14.0	16.1
-140	14.9	15.5
-160	15.1	15.2
-161	14.8	16.5
-187	17.9	18.2
-188	13.9	14.8
-200	12.3	13.8
-201	17.2	18.2
-202	17.1	19.5
-209	12.5	15.9
D- 20	17.1	18.3
A- 30	16.3	19.0
T 141	14.7	14.9
IR 8	15.1	15.6
$\bar{x}$	15.3	16.6
sd	1.35	1.48
cv%	8.83	8.94

Correlation coefficient of N content between Experiment III and IV  
 $r=0.6947^{**}$

- 1) Expt. III performed with 3 replicates from Dec. 20 to 27, 1971.
- 2) Expt. IV performed with 3 replicates from March 15 to 22, 1972.



Eig. 8 Relationship between net assimilation rate and specific leaf weight among rice varieties (Experiment II, Series 5, Sept., 1971).

**Table 19 Analysis of variance on N content per unit leaf area between Experiment III and IV.**

Source	df	ss	ms	F
Total	179	567,056		
Varieties	29	301,365	10,391	8.85**
Expts.	1	76,578	76,578	65.21**
Var. x Expt.	29	48,199	1,662	1.42 <sup>ns</sup>
Error	120	140,914	1,174	

Furthermore, the relationship between total nitrogen content per leaf area and total nitrogen concentration (N% of leaves) was examined. Table 20 shows a dispersed relation between them. Coefficient of variation of the mean nitrogen concentration among varieties was smaller (less than 3%) than that of nitrogen content per unit leaf area (more than 8%).

Based on anatomical studies on rice varieties, Chonan (7) reported that SLW did not relate to morphological thickness but showed a close negative relation to the length of fibrovascular bundle. Watanabe et al. (85) reported that thickness of primary leaf of soybean related closely to fresh weight per unit leaf area, because leaf thickness may indicate vacuole as well as mesophyll cell. Freind et al. (23) described that leaf thickness meant specific leaf weight in studies on wheat. In rice, however, such a relation is not yet observed. Since specific leaf weight of rice relates closely not only to net assimilation rate but also to total nitrogen content per unit leaf area in this study, it is very likely that leaves of rice plants are rich in content of mesophyll cells which undertake photosynthesis.

**Table 20 Nitrogen concentration and nitrogen content per unit leaf area of selected varieties (Experiment IV).**

Exptl. var. no.	N % of leaves <sup>1)</sup>	N content mg N dm <sup>-2</sup> leaves
B— 16	6.16	16.7
— 56	6.27	15.5
— 59	6.15	16.5
— 64	6.37	15.3
— 75	6.32	18.9
— 84	6.36	18.3
— 88	6.34	16.1
—105	6.30	17.1
—113	6.37	17.4
—114	6.02	15.8
—116	6.31	17.3
—117	6.36	14.4
—118	6.38	17.6
—121	6.48	16.7
—132	5.95	15.0
—134	6.31	17.5
—136	6.09	16.1
—140	6.69	15.5
—160	5.96	15.2
—161	6.02	16.5
—187	6.37	18.2
—188	6.33	14.8
—200	6.16	13.8
—201	6.38	18.2
—202	6.18	19.5
—209	6.34	15.9
D— 20	6.30	18.3
A— 30	6.26	19.0
T141	6.56	14.9
IR 8	6.56	15.6
$\bar{x}$	6.29	16.2
sd	0.173	1.48
cv %	2.76	8.94

Correlation coefficient between N % and N content per unit leaf area :

$$r=0.1385^{ns}$$

- 1) Leaves obtained from growth analysis experiment with 3 replicates on March 22, 1972.

Thus, it was made clear that  $SLW_2$  is the character most closely related to NAR among many morphological characters. Varieties with higher NAR have higher  $SLW_2$ . NAR has the relationship of multiple regression to leaf area per leaf blade, tiller size, plant height, SLW, increase of leaf number and increase of leaf area to the extent of 82.1% of all determinant factors. SLW is a character stable against climatic environment and relatively constant in the relative order among varieties grown in any season. SLW can be regarded as a useful criterion in the primary selection for higher NAR varieties. It is also recognized that total nitrogen content per leaf area is closely related to SLW, showing the similar response to climatic environment as SLW. Therefore, this character also may possibly be used as a criterion of selection for higher NAR varieties.

#### 4. Relationship of net assimilation rate between early stage and later stage.

In the previous experiments net assimilation rate was determined at the early stage of plant growth, i.e., at the 5th to 7th leaf age. If the characteristics of net assimilation rate at an early stage of rice varieties does not change at the later stage, the determination of net assimilation rate at the early stage, that can be done easily in growing plant materials and in the measurement, would be sufficient enough to obtain photosynthetic capacity of rice varieties. Therefore, net assimilation rate at the maximum tiller stage was measured and compared with that obtained at the early stage. This experiment is referred to the Experiment V.

##### (1) Materials and methods

The Experiment V was conducted in the field. Seedlings of 8 varieties which had higher or lower NAR were transplanted to a plot of 47 m<sup>2</sup> of area on 17 July, 1972 with 3 replications at 60×60 cm spacing. Fertilizers applied were N-P<sub>2</sub>O<sub>5</sub>-K<sub>2</sub>O (150-50-50 kg per ha). Fifty kg/ha of nitrogen was topdressed 34 days after transplanting. Twenty hills in square were taken as the first sampling at 41 days after transplanting (August, 28) and another 20 hills were taken as the second sampling 7 days after (September, 4). Seven out of 20 hills were selected and 2 of them were measured for leaf area and oven-dried, and the others were oven-dried for total dry weight.

##### (2) Results and discussion

**Table 21 Change of mean total dry weight, leaf area index and number of tillers among 8 varieties in field experiment.**

Varieties	Total dry weight of shoot (g/hill)		LAI		No. of tillers per hill	
	Aug. 28	Sept. 4	Aug. 28	Sept. 4	Aug. 28	Sept. 4
B— 59	7.5	15.9	0.253	0.502	17.3	24.8
— 75	8.8	20.7	0.245	0.496	14.4	18.5
—118	13.9	32.5	0.536	0.952	32.8	50.7
—187	12.0	26.1	0.383	0.689	26.1	33.7
—188	10.9	26.4	0.457	1.008	25.4	39.1
—200	11.0	28.0	0.429	1.093	29.7	37.1
A— 30	9.1	21.2	0.285	0.544	16.4	21.1
IR 8	11.8	24.4	0.445	0.857	32.6	41.8
$\bar{x}$	10.6	24.4	0.379	0.768	24.3	33.4
sd	2.06	5.09	0.107	0.241	7.41	11.1
cv %	19.4	20.8	28.2	31.4	30.5	33.2



Table 21 shows the total dry weight of shoot, leaf area index and numbers of tillers of 8 varieties grown in the field at 41 and 48 days after transplanting. Leaf area index was different from variety to variety, over a range of 0.25 to 0.54 on August, 28 and 0.50 to 1.09 on September 4. Numbers of tillers ranged from 14 to 33 per hill and 19 to 51 per hill at the respective stage. It can be regarded that individual plants were grown as an isolated plant, because LAI was less than 1.09, although number of tillers was relatively large.

It may be difficult to maintain the isolated plant environment without mutual interference after that stage of plants growing in this experiment, because number of tillers and LAI increase, causing the mutual interference among hills.

Table 22 shows NAR at the maximum tiller stage of plants grown in the field of Experiment V in comparison with NAR at the early stage of pot-cultured plants in Experiment III and Experiment IV. It is clearly shown in the table that there are significant differences in NAR among varieties and significant positive relationship of NAR between the Experiment V and III, between Experiment V and IV and between Experiment III and IV. It can be considered that the characteristic of NAR at the early stage is maintained to the maximum tiller stage. NAR at the stage later than the maximum tiller stage was not examined because of the reason mentioned above.

**Table 22 Relationship of net assimilation rate between early stage and later stage (1972).**

Exptl. var. no.	NAR mg dm <sup>-2</sup> day <sup>-1</sup>		
	Field <sup>1)</sup>	Pot <sub>1</sub> <sup>2)</sup>	Pot <sub>2</sub> <sup>3)</sup>
B— 59	91.6	79.1	106.0
— 75	135.3	102.3	103.2
—118	111.0	104.4	122.2
—187	111.3	112.1	120.0
—188	83.6	87.9	106.7
—200	94.6	84.2	95.3
A— 30	125.3	103.6	128.7
IR 8	80.8	83.7	90.0

Correlation coefficient of NAR between :

Field and Pot<sub>1</sub>     $r=0.7719^*$

Field and Pot<sub>2</sub>     $r=0.5675^*$

Pot<sub>1</sub> and Pot<sub>2</sub>     $r=0.7456^{**}$

Analysis of variance on NAR in the field experiment.

Source	df	ss	ms	F
Total	23	14,973.96		
Varieties	7	8,181.96	1,168.85	2.75*
Error <sup>4)</sup>	16	6,792.00	424.50	

1) Field experiment performed at the stage of 41—48 days after transplanting from August 28 to September 4, 1972.

2) Pot<sub>1</sub> (Experiment III) performed on 5—7th leaf stage in pot from December 20 to 27, 1971.

3) Pot<sub>2</sub> (Experiment IV) performed on 5—7th leaf stage in pot from March 15 to 22, 1972.

4) The ss of error contained block-ss because there were no significant difference among blocks.

\* Significant at 10 % level.

It was already clarified in Experiments II, III, and IV that there is a close relationship between NAR and  $SLW_2$ . This relationship was also examined with 8 varieties in Experiment V. Similarly a close positive correlation was found between NAR and  $SLW_2$  or total nitrogen content in the field experiment as given in Table 23. Relationship of specific leaf weight between the field and the pot experiments is shown in Table 24. Although the value of SLW increased according to the progress of growth stage, close positive correlations were found between SLW at any stage of varieties. Especially,  $SLW_3$  related closely to  $SLW_2$  at other stages, although  $SLW_3$  was determined with a single active leaf of each variety at 71 days after transplanting. Table 25 indicates the cor-

**Table 23 Relationship between NAR and  $SLW_2$  or nitrogen content per unit leaf area in the field experiment.**

	$SLW_2$	N content
NAR	0.8933**	0.8257**
$SLW_2$	—	0.9775**

Correlation coefficient computed from each value in Tables 22, 24, 25.

**Table 24 Relationship of specific leaf weight between field and pot experiment.**

Exptl. var. no.	$SLW_1$	$SLW_2$	$SLW_3$	Pot <sub>1</sub> <sup>2)</sup> $SLW_2$	Pot <sub>2</sub> <sup>3)</sup> $SLW_2$
B— 59	3.80	3.96	6.31	2.58	2.67
— 75	4.43	5.31	7.88	2.72	2.99
—118	3.87	4.33	6.40	2.72	2.76
—187	3.80	4.43	5.96	3.01	2.85
—188	3.08	3.65	5.15	2.41	2.35
—200	3.18	3.35	5.28	2.31	2.24
A— 30	3.83	4.76	6.28	2.82	3.03
IR 8	3.49	3.92	5.24	2.38	2.47
$\bar{x}$	3.69	4.21	6.06	2.62	2.67
sd	0.430	0.629	0.899	0.242	0.293
cv %	11.7	14.9	14.8	9.26	11.0

Correlation coefficient of SLW between experiments.

Expts.	Correlation coefficient			
	Field $SLW_2$	Field $SLW_3$	Pot <sub>1</sub> $SLW_2$	Pot <sub>2</sub> $SLW_2$
Field $SLW_1$	0.9216**	0.9501**	0.6747*	0.8821**
Field $SLW_2$		0.9000**	0.7314*	0.9359**
Field $SLW_3$			0.5519	0.7940*
Pot <sub>1</sub> $SLW_2$				0.8690**

- 1) Field experiment performed at the stage of 41—48 days after transplanting (DAT) from August 28 to September 4, 1972.  $SLW_1$ : from whole leaves of 41 DAT plants,  $SLW_2$ : from whole leaves of 48 DAT plants,  $SLW_3$ : from single active leaf of 71 DAT plants.
- 2) Pot<sub>1</sub> (Experiment III) performed on 7th leaf stage in pot from December 20 to 27, 1971.
- 3) Pot<sub>2</sub> (Experiment IV) performed on 7th leaf stage in pot from March 15 to 23, 1972.

**Table 25 Relationship of nitrogen content per unit leaf area between experiments.**

Exptl. Var. no.	N content mg dm <sup>-2</sup> leaves			
	Field <sub>1</sub> <sup>1)</sup>	Field <sub>2</sub>	Pot <sub>1</sub> <sup>2)</sup>	Pot <sub>2</sub>
B— 59	20.1	18.7	16.1	16.5
— 75	24.0	26.8	16.2	18.9
—118	20.6	20.8	15.7	17.6
—187	21.2	22.0	17.9	18.2
—188	17.2	18.4	13.9	14.8
—200	18.3	16.0	12.3	13.8
A— 30	20.8	24.4	16.3	19.0
IR 8	21.4	20.7	15.1	15.6
$\bar{x}$	20.5	21.0	15.4	16.8
sd	2.05	3.43	1.68	1.94
cv %	10.0	16.3	10.9	11.6

Correlation coefficient			
	Field <sub>2</sub>	Pot <sub>1</sub>	Pot <sub>2</sub>
Field <sub>1</sub>	0.8510**	0.6584*	0.7637*
Field <sub>2</sub>	—	0.6826*	0.8987**
Pot <sub>1</sub>	—	—	0.8595**

- 1) Nitrogen content of whole leaves for NAR experiment obtained on August 28 (Field<sub>1</sub>) and September 4 (Field<sub>2</sub>), 1972 in the field.
- 2) Nitrogen content of whole leaves for NAR experiment obtained in Experiment III (Pot<sub>1</sub>) and Experiment IV (Pot<sub>2</sub>) in pot experiments.

relation of total nitrogen contents per unit leaf area at each stage of plants. It is recognized that total nitrogen content per unit leaf area at the maximum tiller stage was higher than that at the early tillering stage but it indicated the similar pattern as that of the early stage. The fact that the varietal difference of SLW and total nitrogen content per unit leaf area, both of which are most closely related to NAR among characters of varieties, at the maximum tiller stage is closely related to that of the early stage is suggestive of the usefulness of measuring these characters at the 5–7th leaf age for the screening of varieties for higher NAR.

#### IV. Net photosynthetic rate of single leaf and its characteristics among varieties

There are many papers reporting varietal differences of net photosynthetic rate ( $P_N$ ) of single leaf as an index of photosynthetic capacity in many crop plants. In general, net photosynthetic rates higher than the past records have been obtained due to the improvement of measuring methods since late 1960's. However, little studies were made by the improved method with *Indica* rice. Therefore, net photosynthetic rate of rice varieties showing apparently varietal difference in NAR was measured, and the relationship between  $P_N$  and NAR was examined in this chapter.

## 1. Varietal difference of net photosynthetic rate of single leaf

Photosynthesis of crop plants is regulated with 3 components; photosynthetic capacity of single leaf, the extent of photosynthesizing surface and the environment of leaves. Net photosynthetic rate of single leaf was measured by the  $\text{CO}_2$  exchange method. The active leaf fully developed but not over-matured was used as the material and  $P_N$  of that leaf was taken as representing photosynthetic capacity. Varietal differences in  $P_N$  and variations of  $P_N$  with different leaf position were examined.

### (1) Materials and methods

Varieties, different in net assimilation rate, were already known by the growth analysis in the previous chapter. Net photosynthetic rate of single leaf was measured with 30 varieties including IR8. The leaf, next to the uppermost leaf, is used when it developed fully, and referred to the "single leaf" hereafter in this paper. In order to measure net photosynthetic rate of the 5–6th leaf (March, 1972) and the 6–7th leaf (May, 1972), 3 plants were grown in Wagner pots (a/5000 of size) fertilized with  $\text{N-P}_2\text{O}_5\text{-K}_2\text{O}$  (1.0-0.5-0.5 g per pot) with 3 replicates. For measuring 9–10th leaf (June 1972), 2 plants were grown in Wagner pots (a/2000 of size) fertilized with  $\text{N-P}_2\text{O}_5\text{-K}_2\text{O}$  (1.5-0.8-1.0 g per pot) with 3 replicates. Top dressing was applied with 0.2 g of nitrogen for a/5000 pot and with 0.5 g of nitrogen for a/2000 pot a week before measurement. For measuring  $P_N$ , an intact leaf was placed in an air-sealed leaf chamber (300L×30W×3T mm) (72, 89), and net  $\text{CO}_2$  exchange was measured by a Plantass D4A Beckman-Toshiba Infrared Gas Analyzer (differential type) and ASSA-2 Horriba Infrared Gas Analyzer (differential type). Fresh air, taken from the atmosphere at 10 m above ground, was supplied to the chamber at a rate of 1.0–6.0 litre per minute with enrichment of moisture through water bottles. The air, passing through the chamber containing the leaf, was nearly dehumidified with a spiral cooler and one litre of the air was used for infrared gas analysis of  $\text{CO}_2$  concentration. The leaf placed in the chamber was fixed at a right angle to the light, which passed through 20 cm layer of water filter. The leaf was exposed preliminarily to 20 K Lux illumination with 3 bulbs of 500 W incandescent lamp per chamber and after the light intensity was increased to the level of light saturation  $\text{CO}_2$  exchange was measured under the condition of 60 K Lux and 30°C of air temperature. For the light induction of leaf, it took 10 to 30 minutes according to conditions.

Since atmospheric  $\text{CO}_2$  concentration fluctuated over a range of 295 to 315 ppm, it was compensated to 300 ppm for the calculation of  $P_N$ . Air was calibrated every one to 3 hours.  $P_N$  was calculated by the method of Hesketh and Moss (30).

### (2) Results and discussion

Since NAR was measured with plants at the 5–7th leaf age,  $P_N$  of the 5–6th leaf and 6–7th leaf was measured in the similar growing period. Table 26 shows varietal differences of  $P_N$  of the 5–6th leaf at 1% level of significance.  $P_N$  of examined varieties ranged from 43.0 to 54.0  $\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$  and the varietal differences of  $P_N$  were indicated by Duncan's multiple range test at 5% level of significance. IR8 was found in a group of lower  $P_N$  varieties. Table 27 also shows varietal differences of  $P_N$  of the 6–7th leaf at 5% level of significance.  $P_N$  ranged from 47.9 to 61.3  $\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ . IR8 was in a group of intermediate  $P_N$  variety. Table 28 shows varietal differences of  $P_N$  of the 9–10th leaf at 1% level of significance.

In order to know the relation of  $P_N$  to different leaf position,  $P_N$  of 20 varieties ex-

**Table 26** Difference of  $P_N$  of the 5—6th active leaves among selected rice varieties (March, 1972).

Exptl. Var. no.	$P_N^{1)}$ mg $CO_2$ $dm^{-2}$ $h^{-1}$	Range test <sup>2)</sup>
B— 56	54.0	a
—132	53.4	a b
— 88	53.2	a b
— 75	52.3	a b
—187	52.2	a b c
—202	52.2	a b c
A— 30	51.2	c d
B—134	51.0	c d
—140	50.8	c d
D— 20	50.5	c d
B— 84	50.2	c d
—116	49.9	d e
— 16	49.9	d e
—136	49.4	d e
—118	49.0	d e
T 141	48.8	e f
B—113	48.6	e f
—160	48.5	e f
—201	48.0	e f g
— 64	47.9	f g
—200	47.5	f g h
—161	47.5	f g h
—121	47.1	f g h i
—114	46.1	g h i j
—105	46.0	h i j
—188	45.5	h i j
—117	45.1	i j
IR 8	45.0	i j
B—209	44.0	j k
— 59	43.0	k

Analysis of variance on  $P_N$ , March

Source	df	ss	ms	F
Total	90	1, 836.61		
Varieties	29	893.03	30.744	2.53**
Error	61	743.58	12.190	

1)  $P_N$  measured with 5—6th leaves from March 20 to 25, 1972, by Beckman-Toshiba IRGA.

2) Duncan's multiple range test at 5 % level.

\*\* Significant at 1 % level.

**Table 27 Difference of  $P_N$  of the 6—7th active leaves among selected rice varieties (May, 1972).**

Exptl. Var. no.	$P_N^{1)}$ mg $CO_2$ dm <sup>-2</sup> h <sup>-1</sup>	Range test <sup>2)</sup>
D— 20	61.3	a
A— 30	60.2	a
B— 84	60.1	a
— 75	57.3	b
— 56	57.1	b
— 59	55.2	b c
— 16	55.2	b c
B—117	55.0	b c d
— 64	54.8	b c d e
— 88	54.4	c d e f
—105	54.3	c d e f
IR 8	54.2	c d e f g
B—113	54.2	c d e f g
—121	54.1	c d e f g
—132	53.7	c d e f g
—116	52.9	c d e f g h
—160	52.6	c d e f g h
—140	52.4	d e f g h
—134	52.2	e f g h
—187	51.9	f g h
—136	51.6	g h i
—202	50.8	h i j
—209	50.6	h i j
—201	50.6	h i j
—188	50.5	h i j
—118	49.3	i j k
—114	49.2	i j k
—200	48.5	j k
—161	47.9	k

Analysis of variance

Source	df	ss	ms	F
Total	90	1,771.35		
Varieties	28	804.15	28.719	1.84*
Error	62	967.20	15.600	

1)  $P_N$  measured with 6—7th leaves with 3 replicates from May 20 to 25, 1972, by Horiba IRGA.

2) Duncan's multiple range test at 5 % level.

\* Significant at 5 % level.

**Table 28** Difference of  $P_N$  of the 9–10th active leaves among selected rice varieties (June, 1972).

Exptl. Var. no.	$P_N^{1)}$ mg $CO_2$ $dm^{-2} h^{-1}$	Range test <sup>2)</sup>
B— 84	55.8	a
— 88	55.6	a b
— 56	55.4	a b c
—134	55.0	a b c
— 75	53.5	a b c d
A— 30	53.3	a b c d e
D— 20	53.2	b c d e
B—187	53.0	d e
—209	52.4	d e f
—132	51.3	d e f
IR 8	50.9	e f g
B— 16	50.3	f g
—113	49.5	g h
—202	48.5	g h
—136	47.6	h i
— 59	45.4	i j
—200	45.4	i j
—121	44.3	i j k
—188	42.8	k l
—118	41.3	l

Analysis of variance

Source	df	ss	ms	F
Total	84	2,003.37		
Varieties	19	1,365.40	71.863	7.32**
Error	65	637.92	9.841	

1)  $P_N$  measured with 9–19th leaves from June 4 to 10, 1972, by Horiba IRGA.

2) Duncan's multiple range test at 5 % level.

\*\* Significant at 1 % level.

amined commonly in these experiments and the relationship of  $P_N$  between each experiment are shown in Table 29. It was recognized that there were significant correlations between  $P_N$  of 5–6th leaves and that of 9–10th leaves, and similarly between 6–7th leaves and 9–10th leaves, although there was no significant relationship of  $P_N$  between 5–6th leaves and 6–7th leaves. The last one is likely to be based on experimental error. It can be considered, therefore, that  $P_N$  of different leaves with different leaf position on the stem was closely related with each other. Table 30 shows the significant difference of  $P_N$  among varieties and among the experiments, indicating that the values of  $P_N$  varied from experiment to experiment. Interaction of varieties-experiment is also recognized implying that the order of varieties with respect to  $P_N$  varies from experiment to experiment. However, such a variation of varietal order is recognized to be occurred only within a range of significant correlation, and similar to the fluctuation of NAR

**Table 29 Relationship of  $P_N$  between experiment (1972).**

Exptl. var. no.	$P_N$ (mg $CO_2$ dm <sup>-2</sup> h <sup>-1</sup> )		
	(Mar. 20—25) 5—6th leaf	(May 20—25) 6—7th leaf	(June 4—10) 9—10th leaf
B— 16	51.5	55.2	50.3
— 56	54.0	57.1	55.4
— 75	55.1	57.3	53.5
— 84	49.4	60.1	55.8
— 88	52.5	54.4	55.6
—113	48.6	54.2	49.5
—118	47.5	49.3	41.3
—121	47.0	54.1	44.3
—132	53.4	53.7	51.3
—134	52.5	52.2	53.5
—136	49.4	51.6	55.0
—187	52.7	51.9	53.0
—202	51.7	50.8	48.5
A— 30	51.0	60.2	53.5
D— 20	51.9	61.3	53.2
B— 59	52.6	55.5	45.4
—188	47.4	50.5	42.8
—200	46.9	48.5	45.4
—209	45.5	50.6	52.4
IR 8	45.3	54.2	50.9
$\bar{x}$	50.3	54.1	50.5
sd	2.94	3.65	4.48
cv %	5.86	6.74	8.86

Correlation coefficient of  $P_N$  between:

- 1) 5—6th and 9—10th leaf  $r=0.5925^{**}$
- 2) 6—7th and 9—10th leaf  $r=0.5291^*$
- 3) 5—9th and 6—7th leaf  $r=0.3200^{ns}$

**Table 30 Analysis of variance of  $P_N$  among experiments (Mar.—May—June 1972).**

Source	df	ss	ms	F
Total	199	4,879,557		
Varieties	19	1,810.110	95.269	9.304**
Experiments	2	671.994	335.997	32.814**
Var. × Expt.	38	961.918	25.314	2.472**
Error	140	1,433.535	10.239	

between experiments as shown in Table 11.

It was reported with *Japonica* rice that the value of  $P_N$  ranged from 7.9 to 12.6 mg  $CO_2$  dm<sup>-2</sup> hr<sup>-1</sup> (50) and was approximately 20 mg  $CO_2$  (60) although the latter was different with leaf position and with experiments. IRRI (33) reported preliminarily that



$P_N$  of *Indica* and a few *Japonica* rice varieties showed a variation over a range of 34.5–62.1 mg CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup>, which contained dark respiration. Takano and Tsunoda (71) recognized that  $P_N$  of 14 varieties of *Japonica* rice distributed over a range of 29–47 mg CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup> and  $P_N$  of 13 varieties of *Indica* rice over a range of 22–47 mg CO<sub>2</sub>. McDonald et al. (44) reported that a variety Blue Belle had the highest  $P_N$  and IR8 had the lowest one among 10 varieties of which  $P_N$  distributed over a range of 42.6–67.4 mg CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup>. Although the data obtained in these studies were not treated by statistical analysis, it can be recognized that there are varietal differences of  $P_N$  in *Japonica* and *Indica* rice. In studies by Murata (50) and Osada (61), the value of  $P_N$  was relatively low because of using detached leaves and the varietal differences were discussed at such a low level of  $P_N$ . Since the present study gave the values similar to those of IRRI (33), Takano and Tsunoda (71) and McDonald (44), it can be said that varietal differences of net photosynthetic rate in *Indica* varieties actually exists.

Ludlow and Wilson (43) examined the temperature hysteresis of  $P_N$  and indicated that grasses and legumes grown at 20°C and measured at 30°C gave  $P_N$  values lower than that of the plants grown at 30°C, but almost complete acclimatization to the higher temperature occurred within 15 hours. In the present study, however, such effect of hysteresis of temperature and solar radiation was not examined. The mean temperature and solar radiation in the experimental period and during a week before that were 25.8°C and 388 ly day<sup>-1</sup> for the 5–6th leaf experiment, 28.2°C and 481 ly day<sup>-1</sup> for 6–7th leaf experiment and 25.8°C and 388 ly day<sup>-1</sup> for the 9–10th leaf experiment. The mean temperature and solar radiation were only a little higher in the 6–7th leaf experiment than in other two experiments.

The result that  $P_N$  of 20 varieties at the 6–7th leaves was slightly higher than those of other leaves as shown in Table 29 might have been caused by higher temperature and higher solar radiation in a period of that experiment than those of other experiments. However, it can be said that the effect was only very small in this case.

With other crops except rice, it has been reported that there were distinct varietal differences of net photosynthetic rate in soybean (12, 14, 15, 56, 58), maize (17, 22, 30), wheat (20, 40, 69), barley (1), oat (11), bean (36) and sugarcane (32). Based on the result of the present study on rice, it was made clear that varietal differences of net photosynthetic rate such as that already found in other crop species actually exist in *Indica* rice.

$P_N$  of the 5–6th leaf showed a range of 43–54 mg CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup> and  $P_N$  of the 6–7th leaf 48–61 mg and  $P_N$  of 9–10th leaf 41–56 mg with 30 varieties examined. Coefficient of variation of  $P_N$  among varieties was over a range of 6.7–10.2%. It was also clarified that order of varietal ranking of  $P_N$  was consistent at different growth stage of plants, without showing a large deviation.

## 2. Plant characters relating to net photosynthetic rate

Net photosynthetic rate measured with a single leaf which represents photosynthetic capacity of the plant ought to relate to photosynthetic rate of a whole plant which is composed of a number of leaves. Since the fully-developed but not over-matured single leaf was used for the measurement of  $P_N$ , the  $P_N$  obtained is regarded as indicating the maximum photosynthetic efficiency of a single leaf. And also since an isolated plant was used for measuring NAR, NAR of the present experiment is regarded as indicating the mean photosynthetic capacity of a whole plant. As it was already shown that NAR

is closely related to certain plant characters, and as  $P_N$  is expected to have a close relation to NAR, a study to identify the plant characters related to net photosynthetic rate was carried out in this section.

(1) Materials and methods

Previous experimental data were used in this section, except total nitrogen was analyzed with the leaves used for measuring net photosynthetic rate according to semi-micro Kjeldhal method.

(2) Results and discussion

The relationship between plant characters of rice and net assimilation rate was already taken up in the previous chapter. Table 31 shows the plant characters which related significantly to net photosynthetic rate. Data of plant characters were those obtained in Experiment III, in which growth stage of plants was the same as that in  $P_N$  measuring experiment. The plant characters found to be closely related to  $P_N$  with 29 varieties except T-141 examined in Table 26 were specific leaf weight ( $SLW_2$ ) and plant height ( $H_2$ ) at the second sampling for NAR measurement, as well as dry matter increase ( $\Delta W$ ) and NAR. Therefore, it can be considered that the variety with higher  $P_N$  is the variety with larger  $SLW_2$ , higher plant height, higher dry matter increase and also higher NAR. These characters may possibly be used as the criteria for screening higher photosynthetic varieties.

**Table 31 Relationship between  $P_N$  and some plant characters.**

Plant character	Correlation coefficient to $P_N$
$SLW_2$	0.430*
$H_2$	0.374*
$\Delta W$	0.386*
NAR	0.528**

Calculated with  $P_N$  values of the 5—6th leaf and with plant characters determined by the Experiments III with 29 varieties.

Since it is clarified that there is a close relationship between  $P_N$  and  $SLW_2$ , the relations between  $P_N$  and specific leaf weight of the leaves used for  $P_N$  measurement ( $SLW_{PN}$ ) and between  $P_N$  and total nitrogen content per unit leaf area were examined as shown in Table 32.  $P_N$  indicated the significantly positive relation to  $SLW_{PN}$  and also

**Table 32 Relationship between net photosynthetic rate and specific leaf weight or nitrogen content per unit leaf area (1972).**

Expts.	Correlation coefficient		
	N content (mg dm <sup>-2</sup> leaf)	$SLW_{PN}$ (mg cm <sup>-2</sup> )	$N \times SLW_{PN}$
$P_N$ 5—6th leaf	0.6868**	0.3570	0.5799**
" 6—7th leaf	0.7401**	0.5857**	0.7258**
" 9—10th leaf	0.7716**	0.5462*	0.5556*
N content 5—6th leaf		0.5716**	
" " 6—7th leaf		0.7816**	
" " 9—10th leaf		0.7488**	

to total nitrogen content per unit leaf area at each leaf age. Furthermore, there was a significant relationship between  $P_N$  and total nitrogen per unit leaf area  $\times$   $SLW_{PN}$ . The correlation between  $SLW_{PN}$  and total nitrogen content per unit leaf area was similar to that between  $SLW_2$  and nitrogen content of leaves used for  $SLW_2$  determination (Fig. 6 and Table 40).

**Table 33 Relationship of  $SLW_{PN}$  between experiments (1972).**

Exptl. var. no.	$SLW_{PN}$ (mg cm <sup>-2</sup> )		
	Mar. 5—6th leaf	May 6—7th leaf	June 9—10th leaf
B— 16	3.35	3.31	3.54
— 56	3.37	3.16	3.67
— 75	3.75	3.89	4.12
— 84	3.57	3.70	3.64
— 88	3.39	3.58	3.35
—105	3.41	3.30	—
—113	3.25	3.40	3.56
—114	3.31	3.34	—
—116	3.15	3.26	—
—117	3.04	3.28	—
—118	3.14	3.34	3.40
—121	3.73	3.23	3.49
—132	3.14	3.54	3.68
—134	3.23	3.32	3.88
—136	3.20	3.37	3.87
—140	2.88	3.25	—
—160	3.38	3.18	—
—161	3.31	3.48	—
—187	3.58	3.84	3.94
—201	3.30	3.96	—
—202	3.44	3.90	3.74
A— 30	3.41	3.72	3.79
D— 20	3.47	3.62	4.05
B— 59	3.09	3.17	3.62
— 64	3.34	3.21	—
—188	2.35	3.08	2.80
—200	2.90	2.84	3.17
—209	3.13	2.90	3.42
IR 8	3.30	3.37	3.53
$\bar{x}$	3.31	3.41	3.61
sd	0.211	0.284	0.307
cv %	6.34	8.33	8.51

Correlation coefficient of  $SLW_{PN}$  between :

- 1) 5—6th and 6—7th  $r=0.5693^{**}$
- 2) 5—6th and 9—10th  $r=0.5291^*$
- 3) 6—7th and 9—10th  $r=0.6593^{**}$

Now, it was reconized that there are close relationships between each of  $P_N$ , SLW of the leaf used for  $P_N$  determination and total nitrogen content per unit leaf area. In Tables 32 to 35, data of  $SLW_{PN}$  and nitrogen content per unit leaf area of the 5–6th, 6–7th and 9–10th leaves are given. Table 33 shows that, although  $SLW_{PN}$  increases according to the advance of leaf position, there are significant correlations of  $SLW_{PN}$  between different leaf position. The analysis of variance of  $SLW_{PN}$  shown in Table 34 indicates 1% level of significance among varieties and experiments but insignificance for interaction of varieties-experiments.

**Table 34 Analysis of variance on  $SLW_{PN}$  among experiments (Mar.—May—June 1972).**

Source	df	ss	ms	F
Total	199	31.270		
Varieties	19	12.533	0.6597	8.59**
Experiments	2	4.466	2.233	29.67**
Var.×Expt.	38	3.520	0.0926	1.21 <sup>ns</sup>
Error	140	10.751	0.0768	

Thus, the order of varietal ranking with regard to  $SLW_{PN}$  was found to be consistently similar with different leaves of different time of emergence, indicating that SLW is one of the most stable plant characters. The similar trend as  $SLW_{PN}$  was observed with total nitrogen content per unit leaf area as given in Table 35.

It was recognized that net photosynthetic rate of varieties showed a significant interaction between varieties and leaf position (or experiments) as shown in Table 30, although specific leaf weight did not show a significant interaction between varieties and leaf position. Net photosynthetic rate is regarded as one of the expression of physiological activities of leaves whereas specific leaf weight is one of the morphological characters of leaves. Measurement of physiological activities is apt to involve errors as compared with measurement of morphological characters. This may explain the occurrence of significant interaction between varieties and leaf position observed with  $P_N$ . Therefore, although the order of varietal ranking was changed partially in different experiments, it can be concluded that basically the variation of varietal order with regard to  $P_N$  in different experiments might be as small as that of  $SLW_{PN}$ .

In the past studies, a close correlation between  $P_N$  and SLW was observed with rice (50), soybean (4, 14, 56), maize (30), oat (11) and alfalfa (62), and also close relationships between  $P_N$  and total nitrogen content per unit leaf area or protein nitrogen content were indicated among varieties of rice (50, 59, 71) and *Solidago virgourea* (3). In the above evidences, the significant correlation between  $P_N$  and SLW or total nitrogen content per unit leaf area was obtained even with leaves of different leaf position of soybean (56) and also the significant correlation of SLW between years was shown in oat (11). These results suggest that SLW, which is an expression of morphological characters of leaf is a relatively stable phenotype against environmental condition even with other crops than rice.

On the other hand, a positive relation was found between  $P_N$  and leaf thickness in sugarcane (32), although there was no positive relation between  $P_N$  and SLW. The positive relation between SLW and morphological leaf thickness was also recognized in

**Table 35 Relationship of nitrogen content per unit leaf area  
between experiments.**

Exptl. var. no.	N content, mg N dm <sup>-2</sup>		
	March 5—6th leaf	May 6—7th leaf	June 9—10th leaf
B— 16	17.6	17.6	15.1
— 56	19.3	17.4	18.9
— 75	20.3	21.2	19.2
— 84	20.0	20.4	17.9
— 88	19.2	17.7	18.7
—105	18.4	17.5	—
—113	18.2	16.8	16.5
—114	18.8	14.9	—
—116	17.7	17.0	—
—117	17.3	18.9	—
—118	18.0	17.5	16.1
—121	17.1	17.1	15.3
—132	15.9	17.2	17.3
—134	19.4	19.0	20.3
—136	17.6	17.9	16.2
—140	18.0	17.4	—
—160	17.3	16.7	—
—161	18.0	17.1	—
—187	19.7	20.7	17.6
—201	17.9	18.1	—
—202	19.0	19.9	17.7
A— 30	18.9	19.8	18.9
D— 20	18.6	19.7	18.7
B— 59	17.3	17.6	17.3
— 64	19.0	17.3	—
—188	16.6	15.4	13.0
—200	16.4	14.4	12.8
—209	17.0	15.9	17.2
IR 8	19.9	18.3	16.8
T 141	17.6	—	—
$\bar{x}$	18.2	17.8	17.1
sd	1.18	1.66	1.97
cv %	6.49	9.31	11.5

Correlation coefficient of  $P_N$  between:

- 1) 5—6th leaf and 6—7th leaf  $r=0.6600^{**}$
- 2) 5—6th leaf and 9—10th leaf  $r=0.6790^{**}$
- 3) 6—7th leaf and 9—10th leaf  $r=0.7112^{**}$

wheat (23, 24) but not in soybean (85). Different results were obtained on the relation between the both characters according to crop species or research workers.

In case of soybean and oat, significant negative correlations were found between  $P_N$  and  $CO_2$  diffusion resistance within leaf, especially stomatal resistance ( $r_s$ ) or mesophyll resistance ( $r_m$ ) (11, 14). Correlation between  $P_N$  and  $r_m$  was also found with some crop species (19). It may thus be suggested that a higher  $P_N$  leaf has lower  $CO_2$  diffusion resistance. On the other hand,  $P_N$  shows a close positive relation to SLW at the same time. In 2 *Lolium* and its 28 varieties, it was recognized that there was the positive relationship between  $P_N$  and numbers of mesophyll cell (N)  $\times$  leaf thickness (T) and the increase of N accompanied the decrease of cross section area of mesophyll cell. Namely, the increase of  $P_N$  occurred when the surface area of mesophyll cell increased or leaf thickness also did (88). The studies may suggest that  $P_N$  connected closely to  $CO_2$  diffusion resistance and mesophyll resistance. At present, accumulation of experimental results with a given crop species is not enough to explain the interrelationship of these factors.

However, Watanabe and Tabuchi (85) recognized that the varietal order with respect to  $P_N$  of primary leaf of soybean did not change in a range of atmospheric carbon dioxide from 340 to 1,700 ppm. In other words, varietal difference of  $P_N$  might have disappeared when atmospheric carbon dioxide concentration was increased, if it is caused mainly by carbon dioxide diffusion resistance. In their experiment, they were not able to recognize that there were close relationships between  $P_N$  and leaf thickness or fresh weight per unit leaf area, and deduced that varietal difference of  $P_N$  might be caused mainly by the activity of chloroplast in primary leaf of soybean. Watanabe's result may be supported by the fact that there was a close relationship between  $P_N$  and activity of RuDP carboxylase in crowns of 2 races of *Solidago virgourea* (3) and in soybean varieties (4) and also between NAR and activity of PEP carboxylase in varieties of C<sub>4</sub>-plant *Cenchrus ciliaris* (76).

Furthermore, Chonan (7) indicated that there was a close negative correlation between NAR and the distance of fibrovascular bundle within leaf in 8 varieties of *Japonica* rice. It may be supposed that this relates closely to the translocation of photosynthetic products, namely, the rate of translocation of photosynthetic products to other metabolic pathways.

Taking all these results into consideration, the mechanisms of the varietal differences in photosynthetic efficiency may probably be considered as follows; 1) Carbon dioxide diffusion resistance relates closely to photosynthetic efficiency. This means the difference of stomatal resistance and mesophyll resistance, which relates to cell number or cell surface per unit volume of mesophyll cells in carbon dioxide diffusion. In this case, carbon dioxide diffusion resistance is closely associated with specific leaf weight negatively. 2) The activity of chloroplast is associated with photosynthetic efficiency as postulated in primary leaf of soybean. Namely, the difference in the activity of chloroplast is an important limiting factor determining varietal difference of photosynthetic efficiency. 3) The distance of fibrovascular bundle is associated with photosynthetic efficiency. These 3 factors may possibly be functioning independently or dependently with each other. Further research on this aspect with many plant species will give a clear picture of mechanisms of varietal difference in photosynthetic efficiency.

In summary, the present experiments made clear that the plant characters which have close positive relation to  $P_N$  were SLW, total nitrogen contents per leaf area, plant

height, dry weight increase and NAR. SLW and total nitrogen content per leaf area were most closely associated with  $P_N$ . Particularly SLW was found to be a very stable characteristic of varieties, showing no appreciable change in the order of varieties with respect to SLW in different experiments using leaves of different leaf position. Therefore, SLW and total nitrogen content per leaf area of single leaf may possibly be used as a criterion for the selection of varieties for higher  $P_N$ , as effectively as the case of using SLW and nitrogen content of whole leaves.

### 3. Relation between net assimilation rate and net photosynthetic rate

Measurement of net assimilation rate requires much time and laborious work, but this method can give an integrated measurement of net photosynthetic activity under a wider range of conditions in the field. On the other hand, net photosynthetic rate can be measured accurately in a short time but this method measures the maximum net photosynthetic capacity in the form of net  $CO_2$  exchange under a set of environmental condition which can be obtained by the type of enclosure used. Relationship between net assimilation rate and net photosynthetic rate, and plant characters involved are discussed in this section.

The calculation was made using data of NAR and related characters obtained in the Experiment III and Experiment IV of chapter III and data of  $P_N$  and related characters obtained in chapter IV. Multiple regression analysis was applied as shown by Kawabata (38).

Table 36 shows relationship between net assimilation rate and net photosynthetic rate. It can be recognized that  $P_N$  of the 5–6th leaf and the 6–7th leaf at the stage when NAR was measured is significantly associated with NAR measured in different seasons, whereas  $P_N$  of the 9–10th leaf was not significantly associated with both NARs. This fact may probably be brought about by following causes; 1) NAR was measured, as a whole, under lower light intensity than saturated one in  $P_N$  measurement. 2) NAR expresses the value from which the respiratory consumption in leaf sheath and root at day and night and that in leaf blade at night was subtracted. 3)  $P_N$  was measured with a single leaf which was fully developed but not over-matured. In this sense,  $P_N$  expresses the maximum rate of photosynthesis, while NAR expresses the mean rate composed of immatured, matured and senile leaves. The large deviation occurred between NAR and  $P_N$  of the 9–10th leaf might have been resulted from the different growing period involved and/or the above 3 causes.

**Table 36 Relationship between net assimilation rate and net photosynthetic rate of selected rice varieties.**

$P_N$	Correlation coefficient	
	NAR	
	Expt. III <sup>3)</sup>	Expt. IV <sup>4)</sup>
5–6th leaf <sup>1)</sup>	0.5140**	0.4487*
6–7th leaf <sup>2)</sup>	0.4899*	0.4077*

1)  $P_N$  measured with 5–6th leaves from March 20 to 25, 1972.

2)  $P_N$  measured with 6–7th leaves from May 20 to 25, 1972.

3) NAR of Experiment III measured from December 20 to 27, 1971.

4) NAR of Experiment IV from March 15 to 22, 1972.

**Table 37 Correlation coefficients between  $SLW_2$  and  $SLW_{PN}$  of selected rice varieties in several experiments.**

$SLW_{PN2}$	$SLW_2^{1)}$	
	Expt. III	Expt. IV
5—6th leaf	0.7592**	0.5748**
6—7th leaf	0.7646**	0.5697**
9—10th leaf	0.5993**	0.6489**

- 1) Specific leaf weight determined with whole leaves at the end of growth analysis experiments. Experiment III performed from December 20 to 27, 1971, and Experiment IV from March 15 to 22, 1972.
- 2) Specific leaf weight of single leaf used for  $P_N$  measurements. 5—6th leaf used for March experiment, 6—7th leaf for May experiment and 9—10th leaf for June experiment.

Table 37 shows the relationship between specific leaf weight from whole leaves ( $SLW_2$ ) and that of leaves used for  $P_N$  determination ( $SLW_{PN}$ ) at 1% level of significance. In this case, there was a close relationship even between  $SLW_2$  from whole leaves at the 7th leaf age and  $SLW_{PN}$  of the 9—10th leaf. As already indicated, specific leaf weight is a stable character of rice varieties, and in fact it showed only a minute variation either with whole leaves growing under different climatic condition or with a single leaf at different leaf position. Multiple regression between plant characters at the growth stage when NAR was measured and NAR was mentioned in the previous chapter. Furthermore, in order to obtain more close regression equation between NAR and plant characters, multiple regression equation of NAR as a dependent variable was calculated. In addition to 24 plant characters shown in Table 13,  $P_N$  was included in the stepwise regression procedure. In this case, the values of  $P_N$  of 29 varieties except a variety T141 in Table 26 were used for the calculation. Table 38 indicates the best equation of multiple regression connected with  $H_2$  ( $X_{13}$ ),  $W_2/T_2$  ( $X_{22}$ ),  $LA_1/\text{leaf}$  ( $X_{24}$ ) and  $P_N$  ( $X_{26}$ ) with the significant total F value and significant partial F values. The contribution percentage of each plant character (independent variable) to NAR, calculated from the standard partial regression coefficient, shows 40% for  $LA_1/\text{leaf}$ , 26% for  $H_2$ , 20% for  $P_N$  and 14% for  $W_2/T_2$ . In other words, the above plant characters, namely, the mean leaf area per blade at the first sampling, plant height at the second sampling, a stem and leaf dry weight at the second sampling and  $P_N$  of a fully developed leaf are important determinant factors of NAR. This equation fitted at 96.4% to theoretical one. The deviation of  $\hat{Y}$  to  $Y$  was shown in Fig. 9. The measurement of  $H_2$ ,  $W_2/T_2$ ,  $LA_1/\text{leaf}$  and  $P_N$  of the same stage may possibly substitute for the direct observation of NAR with a probability of 86.4%.

Murata (51) recognized that there were close relationships between photosynthetic rate of canopy and its net assimilation rate. Osada (61) indicated that there were close relationships, in 4 out of 7 experiments, between net assimilation rate and photosynthetic rate of single leaf in *Japonica* rice. Such a relation did not exist when different ecotypes of *Dactylis glomerata* L. were grown at different light intensities (75). There was no clear correlation between net assimilation rate and net photosynthetic rate among 13 ecotypes of *Cenchrus ciliaris* L. (76). In general evidences showing the close relationship between net assimilation rate and net photosynthetic rate are scarce. However,



**Table 38 Multiple regression analysis of 27 plant characters including net photosynthetic rate against net assimilation rate by stepwise regression procedure.**

$$\hat{Y}^* = 14.438 + 0.739X_{13} + 0.081X_{22} - 7.056X_{24} + 1.344X_{26}^{1)}$$

$$R^2 = 0.8635$$

Analysis of variance

Source	df	ss	ms	Overall F
Total	28	3,020.95		
Regression	4	2,608.61	652.15	37.96
Residual	24	412.34	17.18	

Coefficients and partial F, etc.

Var. no.	Mean	Std. coeff.	Partial coeff. B	Std. error of B	Partial F test
X <sub>13</sub> (H <sub>2</sub> )	48.97	0.5036	0.7392	0.1750	17.85
X <sub>22</sub> (W <sub>2</sub> /T <sub>2</sub> )	144.37	0.2724	0.0807	0.0410	3.87
X <sub>24</sub> (LA <sub>1</sub> /leaf)	4.53	-0.7783	-7.0558	0.8942	62.27
X <sub>26</sub> (P <sub>N</sub> )	48.93	0.3814	1.3440	0.2866	21.99
Constant term in regression equation = 14.4378					

Contribution of independent variables to  $\hat{Y}$

H <sub>2</sub>	(X <sub>13</sub> );	26.0%
W <sub>2</sub> /T <sub>2</sub>	(X <sub>22</sub> );	14.1
LA <sub>1</sub> /leaf	(X <sub>24</sub> );	40.2
P <sub>N</sub>	(X <sub>26</sub> );	19.7

- 1) X<sub>13</sub>: plant height at the second sampling (H<sub>2</sub>, cm), X<sub>22</sub>: plant dry weight/tiller at the second sampling (W<sub>2</sub>/T<sub>2</sub>, mg/tiller), X<sub>24</sub>: leaf area/leaf at the first sampling (LA<sub>1</sub>/leaf, cm<sup>2</sup>/leaf), X<sub>26</sub>: net photosynthetic rate (P<sub>N</sub>, mg CO<sub>2</sub> dm<sup>-2</sup> h<sup>-1</sup>), Y: net assimilation rate (d.w. mg/dm<sup>2</sup>/day). Data based on Experiment III and P<sub>N</sub>, March.

\* Multiple regression analysis by stepwise regression procedure coded by K. Kawabata with HITAC 8000 in the Computing Center of the Agriculture, Forestry and Fisheries Research Council, Ministry of Agriculture and Forestry, Japan.

the present study demonstrated with *Indica* rice varieties that the net photosynthetic rate of a single leaf growing at the stage when NAR measurement was made coincided fairly well with NAR which expressed the mean photosynthetic capacity. Since there was close relation between specific leaf weight of whole leaves and that of a single leaf of rice varieties (Table 37), basically, the net assimilation rate must be closely associated with net photosynthetic rate of varieties. The deviation between both measurements not conducted at the same growth stage may probably be resulted from 3 causes above-mentioned. Net assimilation rate is such a stable character that it shows approximately the same heritability with varieties grown at different seasons. In addition, as NAR is regarded as expressing the mean photosynthetic capacity of plants growing under natural environment, NAR can be considered to represent more realistic photosynthetic capacity than the net photosynthetic rate does.

Table 39 List of selected varieties with higher NAR and P<sub>N</sub>.

Expt. no.	Acc. no.	Variety name.	Origin	Higher NAR. V.	Higher P <sub>N</sub> V.
B— 75	9,839	JBS 377B	India	**1)	***1)
— 84	7,750	Kaluheenati	Sri Lanka	*	***
—132	7,897	MLY VI 283	Nigeria		***
—134	6,114	Molaga Samba G18	Sri Lanka	**	***
—187	6,728	Radin Edoss 33	Malaysia	**	**
—202	115	Siam	Taiwan	**	*
D 20	154	M 302	Sri Lanka	**	***
A 30	6,711	White China	Fiji Island	**	***

1) Higher photosynthetic efficiency (\*) is indicated by frequency of occurrence for higher NAR or higher P<sub>N</sub> values throughout 5 experiments.

Table 39 shows 8 varieties with higher photosynthetic capacity selected from 301 varieties based on the result of NAR and P<sub>N</sub> measurement. These varieties will be useful as breeding materials in obtaining improved varieties of *Indica* rice with higher photosynthetic efficiency.

The results obtained are summarized as follows: P<sub>N</sub>, which is regarded as expressing maximum photosynthetic capacity, was significantly associated with NAR which expresses a mean photosynthetic capacity of a whole plant, when P<sub>N</sub> and NAR were determined at the same growth stage. SLW of a single leaf was closely associated with SLW of whole leaves. The close relations found between SLW and NAR and between SLW and P<sub>N</sub> underpin the close relation between NAR and P<sub>N</sub>. NAR can be estimated with the multiple regression equation composed of following major variables; leaf area per blade, plant height, P<sub>N</sub> and tiller size. Eight varieties of *Indica* rice with higher photosynthetic efficiency were selected as gene sources from 301 varieties examined.

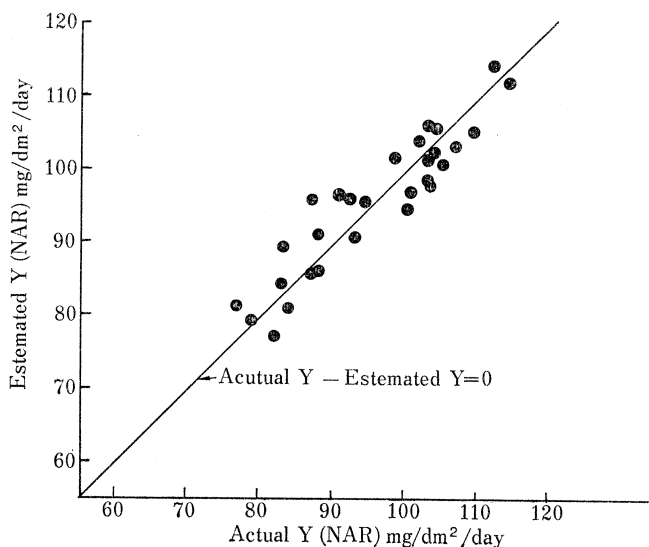


Fig. 9 Deviation of actual NAR from estimated NAR calculated by the multiple regression equation.

$$(\hat{Y} = 14.438 + 0.739X_{13} + 0.081X_{22} - 7.056X_{24} + 1.344X_{26})$$

## V. Relation between leaf area and photosynthetic efficiency in dry matter production

In the previous chapter, the varietal difference of photosynthetic efficiency in *Indica* rice was clearly shown based on varietal difference in net assimilation rate and net photosynthetic rate. In the present chapter relations of photosynthetic efficiency per unit leaf area to the dry matter production of a whole plant as well as the relation between leaf area and photosynthetic efficiency in the dry matter production will be discussed.

### 1. Net assimilation rate and other growth components in growth analysis

Leaf area ratio (LAR) and relative growth rate (RGR) (41, 64) which were correspondent to NAR in growth analysis were examined among varieties. Data of the Experiments II, III and IV were used in this section.

Table 40 and Fig. 10 show the relation between NAR and other growth components or plant characters in growth analysis. Significant positive relationship was observed between NAR and RGR in 5 experimental series in the Experiments II, III and IV. Also there was significant negative relationship between NAR and LAR in all the experiments. Namely, a variety with higher ability of dry matter production per unit leaf area is the one with higher ability of dry matter production per unit dry weight. Since a variety with higher NAR has a smaller LAR, it can be said that a variety with smaller leaf area per unit dry weight is the variety with a higher NAR. As previously mentioned in the Experiments III and IV, there is a close relationship between NAR and  $SLW_2$  (Table 40).

Murata (51) indicated with *Japonica* rice varieties that NAR was closely associated with RGR at the seedling stage and at an early stage after transplanted. Osada (61) also recognized that there was extremely close relationship between NAR and RGR among *Japonica* rice varieties at different growth stage irrespective of the relation between  $P_N$

**Table 40 Relationship between net assimilation rate and relative growth rate or other plant characters.**

Experiment	NAR:RGR	NAR:LAR	NAR: $SLW_2^{4)}$
Expt. II <sup>1)</sup>			
Series 1	.4342**	— .6700**	.6100**
2	.8341**	— .4918**	.1789
3	.8063**	— .6020**	.3813**
4	.4682**	— .8343**	.9071**
5	.4885**	— .7106**	.5648**
Expt. III <sup>2)</sup>	.5268**	— .8118**	.7172**
Expt. IV <sup>3)</sup>	.4266**	— .7511**	.7884**

- 1) Experiment II composed of 5 different experimental series which used different varieties of the original list and were performed from May to September, 1971.
- 2) Experiment III performed on 47 varieties selected in Experiment II from December 20 to 27, 1971.
- 3) Experiment IV performed on 30 varieties selected in Experiment III from March 15 to 22, 1972.
- 4) Specific leaf weight obtained from the second sampling of growth analysis.

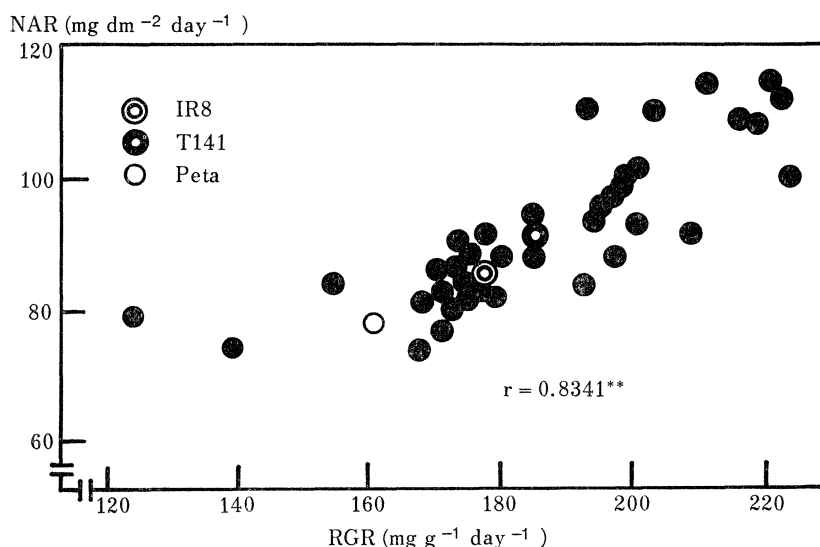


Fig. 10 Relationship between net assimilation rate and relative growth rate among rice varieties (Experiment II, Series 2, June, 1971).

and RGR. Furthermore, the similar relation was observed among 8 ecological types of *Lolium* (88) and among 14 ecological types of *Cenchrus ciliaris* (76). The present study demonstrates that there is the close relationship between NAR and RGR measured under different climatic environment with *Indica* rice varieties. Therefore, the possibility of increasing dry matter production by the improvement of photosynthetic efficiency of *Indica* rice should be emphasized.

## 2. Effect of varietal difference of leaf area and photosynthetic efficiency on dry matter production

The dry matter production of crop plants must be closely associated with leaf area and net photosynthetic rate of single leaf or net assimilation rate. In this section, it was attempted to evaluate the effect of varietal difference in net assimilation rate as a photosynthetic efficiency and in leaf area with *Indica* rice grown under the conditions of isolated plants without mutual competition.

Data of 47 varieties used in the Experiment III (some varieties with 2 replications and others with 3 replications) were used for calculation.

The relation between the dry matter increase and the mean value of leaf area in that experimental period gives the significant correlation coefficient,  $r=0.875^{**}$ , but the relation between the dry matter increase and net assimilation rate as a photosynthetic efficiency is not significant ( $r=0.217$ ). This result suggests the importance of leaf area in dry matter increase, but the role of photosynthetic efficiency is not so clear.

Table 41 indicates the single regression equation in which the dry matter increase was associated with leaf area, and the double regression equation in which the dry matter increase was associated with leaf area and net assimilation rate. Standard partial coefficients of each independent variable were shown at 0.1% level of significance in both regression equations. The determinant coefficient of  $\hat{Y}_2$  containing leaf area and net assimilation rate was higher than that of  $\hat{Y}_1$  containing leaf area only. Namely, the

**Table 41 Multiple and single regressions among dry matter increase, leaf area and net assimilation rate of 47 varieties.**

$$\hat{Y}_1 = 44.95 + 4.955^{***}X_1$$

$$\hat{Y}_2 = -322.79 + 5.57^{***}X_1 + 3.499^{***}X_2^{1)}$$

	Determination coefficient $R^2$	Std. partial regression coefficient	
		$b'Y_{1.2}$	$b'Y_{2.1}$
$\hat{Y}_1$	0.7662		
$\hat{Y}_2$	0.8927	0.951	0.436

Percent contribution of NAR and leaf area to dry matter increase is:

$$\text{NAR: } \frac{0.436}{0.951 + 0.436} \times 100 = 31\%$$

$$\text{Leaf area: } 100 - 31 = 69\%$$

$$\hat{Y}: \Delta W \text{ (mg plt}^{-1}\text{)}, X_1: (LA_1 + LA_2)/2 \text{ (cm}^2 \text{ plt}^{-1}\text{)}, X_2: \text{NAR mg dm}^{-2} \text{ day}^{-1}$$

- 1) The data of 47 varieties obtained at 5-7th leaf stage from December 20 to 27, 1971, at Experiment III were used.

\*\*\* Significant at 0.1% level.

dry matter increase for a given period can be explained much more rationally by the equation including both of leaf area and NAR. In this case, the percent contribution of photosynthetic efficiency ( $X_2$ ) and leaf area ( $X_1$ ) to dry matter increase is 31% and 69% respectively, as obtained from the standard partial regression coefficient.

Namely, the dry matter increase of isolated plants of 47 varieties was shown to be composed of 2 major portions: 30% of it contributed by photosynthetic efficiency and 70% of it contributed by leaf area. Furthermore, Table 42 shows the regression equation of total dry weight at the second sampling to leaf area and NAR in the same experiment. The result gave the similar equation, determinant coefficient and contribution as those shown in Table 41.

**Table 42 Multiple and single regressions among total dry weight, leaf area and net assimilation rate in different 47 varieties.**

$$\hat{Y}_1 = 70.01 + 3.996^{***}X_1$$

$$\hat{Y}_2 = -302.25 + 4.362^{***}X_1 + 3.578^{***}X_2^{1)}$$

	Determination coefficient $R^2$	Std. partial regression coefficient	
		$b'Y_{1.2}$	$b'Y_{2.1}$
$\hat{Y}_1$	0.7700		
$\hat{Y}_2$	0.8975	0.957	0.364

Percent contribution of NAR and leaf area to dry matter production.

$$\text{NAR: } \frac{0.364}{0.957 + 0.364} \times 100 = 28\%$$

$$\text{Leaf area: } 100 - 28 = 72\%$$

$$\hat{Y}: \text{total dry weight (mg plt}^{-1}\text{)}; X_1: \text{total leaf area (cm}^2 \text{ plt}^{-1}\text{)}; X_2: \text{NAR (mg dm}^{-2} \text{ day}^{-1}\text{)}$$

- 1) The data of 47 varieties obtained at 5-7th leaf stage from December 20 to 27, 1972, at Experiment III were used.

\*\*\* Significant at 0.1% level.

Grain yield results from the product of total dry weight and harvest index. Thus, the increase of grain yield depends upon increase of total dry weight or increase of harvest index. A number of studies showed that leaf area development is more important in dry matter production than photosynthetic rate per unit leaf area (17, 74, 84). Up to the present time, experimental evidence showing directly that the increase in yield potential of varieties is associated with the increase in photosynthetic rate have not been reported.

In the present study, in fact, the leaf area contributed to dry matter production much more than the net assimilation rate. However, it was also made certain that the net assimilation rate, which significantly relates to net photosynthetic rate, contributed to dry matter production to a large extent. Now, by putting the data of IR8 obtained in the Experiment III into the regression equation,  $\hat{Y}_2$ , in Table 42, the effect of a varietal improvement, in which photosynthetic efficiency is increased but leaf area is kept constant, on dry matter production was computed. As shown in Table 43, if a variety which has 90 mg dm<sup>-2</sup> day<sup>-1</sup> of NAR and 103 cm<sup>2</sup> plant<sup>-1</sup> of leaf area could be improved

**Table 43 Estimated increment of dry matter production to be caused by an increase in photosynthetic rate of a single plant in a vegetative period.**

NAR <sup>1)</sup> mg dm <sup>-2</sup> day <sup>-1</sup>	% increase of NAR	$\hat{Y}_2$ <sup>2)</sup> mg plt <sup>-1</sup>	% increase of dry matter production
90	—	470	—
108	20	534	14
117	30	567	21
126	40	599	27
135	50	632	35
180	100	792	69
270	200	1,114	137

LA cm <sup>2</sup> plt <sup>-1</sup>	% increase of LA	$\hat{Y}_2$ <sup>3)</sup> mg plt <sup>-1</sup>	% increase of dry matter production
103	—	470	—
124	20	550	19
134	30	605	29
144	40	648	38
155	50	695	48
206	100	920	96
309	200	1,370	192

$$\hat{Y}_2 = -302 + 4.36X_1 + 3.58X_2$$

$X_1$  = leaf area (cm<sup>2</sup> plt<sup>-1</sup>)

$X_2$  = NAR (mg dm<sup>-2</sup> day<sup>-1</sup>)

$\hat{Y}_2$  = total dry matter produced mg plt<sup>-1</sup>

1) NAR was based on IR 8 in Experiment III.

2)  $X_1$  was fixed in 103 cm<sup>2</sup> plt<sup>-1</sup> whose leaf area was IR 8 in Experiment III.

3)  $X_2$  was fixed in 90 mg dm<sup>-2</sup> day<sup>-1</sup>.

to a new variety which has NAR increased by 20%, the dry matter production will be increased from 470 to 534 mg plant<sup>-1</sup> day<sup>-1</sup>. That is an increase of dry matter production by 14%. Furthermore, if NAR could be increased by 40% or 100%, the dry matter production will be increased by 27% or 69% respectively. On the other hand, if the above variety could be improved to a variety which has leaf area increased by 20%, without an increase in photosynthetic efficiency, the dry matter production will increase from 470 to 550 mg plant<sup>-1</sup> day<sup>-1</sup>, which is an increase by 19%. If leaf area increases by 40% or 100%, dry matter production will increase by 38% or 96% respectively. Since this relation was obtained with the plants growing under the experimental condition of isolated plants, the above estimation may probably indicate the upper limit of possibility in varietal improvement, if these 47 varieties used represent the general level of photosynthetic efficiency of *Indica* rice varieties. However, this experimental formula is only applicable to isolated plants within a range of NAR and leaf area shown in the Experiment III. It is not a general formula for estimating dry matter production of plant population over a wider range of growth stage because the influence of mutual shading is not considered in this formula.

The increased photosynthetic rate gives the increase of dry matter production as understood from the above estimation. However, the effect of leaf area on dry matter production is much greater than that of photosynthetic rate. Therefore, with plant populations growing in fields with leaf area lower than the critical LAI, the yield increase can be expected by agronomic practices or breeding approaches that can increase leaf area. On the other hand, varietal improvement with respect to photosynthetic rate may possibly bring more increased yield with plant populations having leaf area greater than the critical LAI.

Excepting the case of an insufficient leaf area due to insufficient planting density, the leaf area below the critical LAI is widely observed in farmers' paddy fields in the tropics at present, owing generally to the shortage of fertilizers. Such a small leaf area causes insufficient yield components, and hence lower grain yields. Under that condition, it is an important problem how to increase leaf area and consequently yield components in order to increase grain yield. Thus, the breeding target is to develop varieties which can produce more leaf area and more yield components at a low level of nitrogen fertilizer. These varieties may not possibly have a high yielding capacity such as that of present high yielding varieties. The average yield of paddy in Southeast Asian countries, at present, is about 1.3 ton per ha (21, 66). From the point of dry matter production, varieties with larger leaf area per unit dry weight, i.e., the varieties with smaller SLW are considered to be effective in increasing yields under the cultural condition prevailing in Southeast Asian countries. Thus, the varieties which have large leaf area per unit dry weight, namely, thin leaves and many tillers at a low nitrogen level are regarded as the breeding target at present.

However, there are, of course, many other approaches to the increased grain yields of rice. The increase of the harvest index is another way to get higher grain yields. If the distribution of photosynthetic product to ears is more effective, the more increased grain yields can be expected without any improvement of photosynthetic efficiency.

It was recognized with soybean leaf that the photosynthetic rate was extremely increased depending upon light intensity when the atmospheric carbon dioxide concentration was increased (5). It was also known that grain yield of rice was increased through the increased rate of dry matter production (CGR) and increased number of

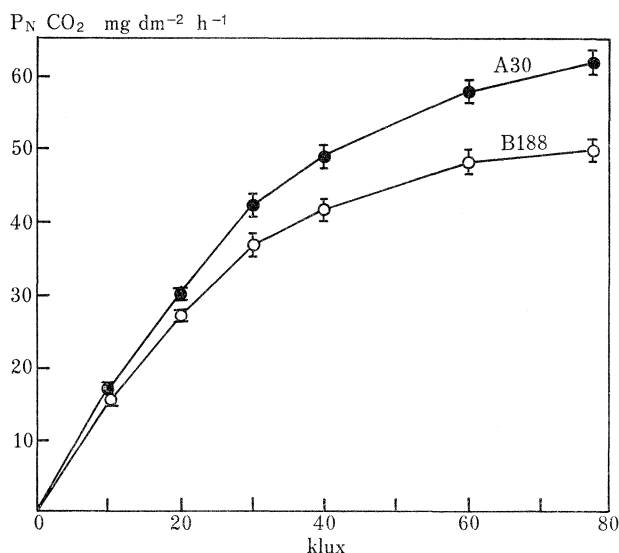


Fig. 11 Net photosynthetic rate measured at 6 different light intensities with the 8th leaf of 2 varieties with higher or lower  $P_N$ .

grains if rice was grown at higher atmospheric carbon dioxide for a period from panicle initiation to flowering. When the carbon dioxide treatment was given after the flowering stage, CGR and weight of 1000 grains were increased (93). The similar result was obtained with soybean (10). Here again, it is proved that the increased photosynthetic rate brings about the increment of yield components and resultant grain yield increases. This suggests the possibility of increasing grain yield by improving photosynthetic efficiency in rice. Therefore, the introduction of the gene for higher photosynthetic efficiency into other varieties with adequate plant characters is another way to increase a yield potential of rice.

High yields of *Indica* rice so far recorded, that are regarded as nearly ceiling, were obtained with leaf area beyond the critical LAI (93). With such plant populations, more yields can be expected by the improvement of photosynthetic efficiency. Although the problems of structure of rice population were not discussed in the present paper, it can be said that it is necessary to add higher photosynthetic efficiency to rice population with ideal structure.

The fact that the variety with high net photosynthetic rate can give the higher rate at any light intensity than that of the variety with low rate is shown with *Indica* as recognized in the light-photosynthesis curve in Fig. 11, as well as by examples of *Japonica* rice (71), *Phaseolus vulgaris* L. (36) and soybean (12). Therefore, it is quite likely that such variety may be able to keep higher photosynthetic rate even inside the population with higher leaf area index. As the varieties with higher photosynthetic efficiency are characterized by the larger SLW and smaller LAR, as demonstrated in the present study, these varieties may not probably have excessive leaf area index in a population as compared with ones with lower photosynthetic rate.

In summary, the present study on the effect of varietal difference of leaf area and photosynthetic efficiency on dry matter production revealed that the partial contribution



of the net photosynthetic rate to the dry matter production was about 30%, whereas that of leaf area was nearly 70% of the total dry matter production.

Therefore, with plant populations which have leaf area smaller than the critical LAI, any measure to increase leaf area will be effective in increasing grain yields. The leaf area can be increased by an increased planting density or by fertilizer application. At the same time, the development of varieties characterized by large leaf area per unit dry weight, i.e., the varieties with small SLW, that are able to increase their LAI at a low level of nitrogen supply is regarded as the useful approach of varietal improvement for the most of the paddy fields of Southeast Asian countries. On the other hand, when plant populations have large leaf area beyond the critical LAI, the varietal improvement to increase photosynthetic efficiency becomes to be an important way to increase grain yield of rice.

## VI. Summary

In the studies on varietal differences of photosynthetic efficiency and dry matter production of *Indica* rice, the followings were clarified:

- 1) Measurement of net assimilation rate under the condition of isolated plants without mutual interferences was obtained by planting 10–20 seedlings per pot (Wagner pot with a size of a/2000) at the 2nd leaf stage, and by taking a half of the plants for the first sample at the 5th leaf stage, followed by the second sampling of remaining plants at the 7th leaf stage after a week.
- 2) Net assimilation rates of 301 varieties was measured under the such growing condition. The frequency distribution of net assimilation rate of varieties examined showed nearly a normal distribution, in which IR8 was located at about the middle point of the distribution. Range of the varietal differences of net assimilation rate as expressed by the ratio of the maximum value to the minimum one and to the value of IR8 was 144–182% and 122–147% respectively, with varieties grown under the same climatic environments. Furthermore, varietal differences of net assimilation rates were proved statistically with varieties examined more in detail.
- 3) Net assimilation rate of varieties measured at different climatic condition gave not only a significant correlation between NAR obtained under 2 different climatic conditions but also nearly equivalent heritability. Thus, net assimilation rate as a photosynthetic efficiency can be obtained irrespective of growth season either in the wet season or in the dry season of the tropics.
- 4) Net assimilation rate was closely associated with specific leaf weight determined with whole leaves out of many morphological plant characters. Specific leaf weight (SLW) was a stable character so that the order of varietal ranking with respect to specific leaf weight was not changed under different climatic environments. Total nitrogen content per unit leaf area was also closely associated with specific leaf weight. In the estimation of net assimilation rate from specific leaf weight, it was recognized that the latter can explain 52% of the variation of net assimilation rate. Thus, specific leaf weight can be used as a primary index for selecting varieties with higher net assimilation rate. Furthermore, net assimilation rate can be estimated to an extent of 81% by the multiple regression equation composed of plant characters such as leaf area per

blade, tiller size, plant height, specific leaf weight, leaf area increase and increase of number of leaf.

5) Net assimilation rate of isolated plants at the maximum tiller stage showed the similar varietal difference as that in the early tillering stage. Also it was closely associated with specific leaf weight and total nitrogen content per unit leaf area. Thus, varietal characteristics with regard to net assimilation rate as a photosynthetic efficiency can be determined at an early growth stage, i.e., the 5th–7th leaf age of the early tillering stage.

6) It was clarified with the statistical significance that there were varietal differences in net photosynthetic rate ( $P_N$ ) in *Indica* rice, based on the measurement of  $CO_2$  exchange rate of intact single leaf. With 30 varieties examined,  $P_N$  ranged 43–54  $mg\ dm^{-2}\ day^{-1}$  at the 5–6th leaf, 48–61  $mg$  at the 6–7th leaf and 41–56  $mg$  at the 9–10th leaf. The coefficient of variation of  $P_N$  among varieties was at a range of 6.7–10.2%. Varietal order of  $P_N$  did not show a large deviation even among different growth stages.

7) Plant characters which have close positive relations to  $P_N$  were SLW, total nitrogen content per unit leaf area, plant height, dry weight increase and NAR. SLW and total nitrogen content per leaf area of a single leaf (which refers a fully-developed but not over-matured leaf, next to the topmost leaf) were closely associated with  $P_N$ . Varietal characteristic of SLW was expressed consistently with leaves of different leaf position. SLW and total nitrogen content per leaf area of a single leaf can be used as a criterion in the selection for higher  $P_N$ , because they are closely related to SLW and total nitrogen content per leaf area of whole leaves.

8)  $P_N$  which is regarded to express the maximum photosynthetic capacity was significantly associated with NAR which expresses a mean photosynthetic efficiency when both were measured at the same stage. NAR can be estimated from the multiple regression equation composed of variables; leaf area per blade, plant height,  $P_N$  and tiller size.

9) Net assimilation rate related positively to relative growth rate (RGR) and negatively to leaf area ratio among varieties. Namely, positive relation between NAR and RGR indicates that an increase of NAR is an important factor in increasing dry matter production.

10) Based on the analysis of the effect of varietal difference of leaf area and net photosynthetic rate to dry matter production, it was recognized that the partial contribution of net photosynthetic rate to dry matter production was nearly 30% whereas that of leaf area was nearly 70% of the total dry matter production. Thus, under field conditions of plant population with leaf area below the critical leaf area index, any measures to increase their leaf area will be effective in increasing yields. Although the leaf area can be increased by increasing planting density and fertilizer application, the development of varieties which are characterized by large leaf area per unit dry weight, i.e., the varieties with small SLW that are able to increase their LAI at a low level of nitrogen supply is regarded as an useful approach for most of the present rice culture in Southeast Asian countries. On the other hand, the varietal improvement to increase photosynthetic efficiency may possibly be an important way to raise further grain yields with plant populations having leaf area index higher than the critical LAI.

11) From the above experimental results, 8 varieties of *Indica* rice that have very high NAR and  $P_N$  were selected. They may serve as the breeding material in developing new varieties with higher yielding potential than so far attained.

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