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〈Invited Lecture〉

Varietal Differences of Photosynthesis and Grain Yield in Rice(*Oryza sativa* L.)[1)]

Ryuichi Ishii*

In the last 100 years, the grain yield per unit land area of rice in Japan increased to about double level (Fig.1). This rapid increase of the rice yield would be attributed to ;

1. Much application of chemical fertilizers, especially nitrogenous one.
2. Efficient control of diseases or insects with agricultural chemicals.
3. Improvement of cultivation technology as exemplified by intensive water management or use of protection nursery bed.
4. Varietal improvement by breeding.

As to the varietal improvemnt, the development of the resistant varieties against diseases or environmental stresses contributed much to the increase of rice yield. But, it is without saying that the breeding to aim at the high yielding itself also played an important role to the increase of rice yield in Japan.

It is generally considered that grain yield of rice can be determined by the rate of dry matter production and its partitioning ratio to the grain. The rate of dry matter production would be determined by the integrated amount of apparent canopy photosynthesis per unit land area (CPS), which consists of three parameters, apparent photosynthetic rate per unit leaf area (LPS), leaf area index (LAI), and light intercepting efficiency. The last two parameters, especially light intercepting efficiency has so far been appreciated as an important high yielding characteristic. However, the first parameter, LPS has never been paid attention in the breeding progress of high yielding varieties, although it can be theoretically expected that LPS would contribute to the increase of grain yield. This expectation,

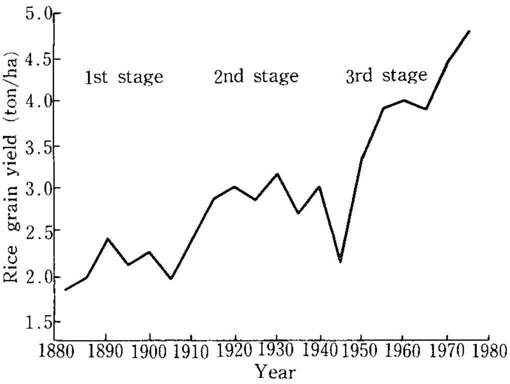

Fig. 1. Incresing trend of rice yield in Japan

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*Faculty of Agriculture, University of Tokyo, Bunkyo-Ku, Tokyo 113, Japan

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The contents of this presentation originate from the following papers presented in the annual meeting of the Crop Science Society of Japan. The full papers are now in preparation.

1. Ishii, R., A.Matsuzaki, W-J.Li, K.Kariya, H.Machida, T.Nakamoto, A.Kumura, and K.Tsunoda. 1986. Studies on the varietal difference of grain yield in rice plants. (I) Yearly change of varietal difference. Japan. Jour. Crop Sci. 55(Extra iss.2) : 65-66.
2. Ishii, R., A.Nagao, H.Sasaki, and A.Kumura. 1986. Studies on canopy photosytnesis in rice plants.(I) Varietal difference. Japan. Jour. Crop Sci. 55(Extra iss.2) : 81-82.
3. Sasaki, H., R.Ishii, and A.Kumura. 1986. Studies on the varietal difference of single leaf photosythesis in rice plants.(I) Varietal difference of photosynthesis at different growth stages. Japan. Jour. Crop Sci.55(Extra iss.2) : 83-84.
4. Sasaki, H., R.Ishii, and A.Kumura. 1987. ________. (II) Stability of single leaf photosynthesis. Japan. Jour. Crop Sci. 56(Extra iss.1) : 94-95.

for an example, was actualized by the work of Yoshida (1973) that the grain yield of rice increased through the LPS accellerated by the raised CO2 concentration in the air.

On the other hand, Evans and Dunstone (1970) reported that in the evolutionary progress of *Aegilops* and *Triticum* species toward bread wheat (*Triticum aestivum*), LPS decreased gradually, and the flag leaf got to increase. Furthermore, it was reported in rice too, that LPS has not necrssarily been improved through its domestication process (Cook and Evans 1983).

In this way, there have been many papers reporting the varietal difference of LPS in relation to grain yield of rice (Hayami 1982, 1983 ; Hayashi 1969 ; Haysahi and Ito 1962 ; Hayashi et al 1977 ; Ito and Hayashi 1969 ; Murata and Osada 1959 ; Murty et al 1973 ; Ohno 1976 ; Osada and Murata 1965a, b), in wheat (Rawson et al 1983 ; Wada et al 1986a, b), or in soybean (Dornhoff and Shibles 1970 ; Wells et al 1982). However, the definite conclusiȯn for the feasibility that LPS can be the breeding criteria for the high yielding varieties, has not yet been reached. One of the factors which prevented us to approach to the definite conclusion, seemed to be the lack in the suitable measuring system of photosynthesis for rapid use in the field condition. So, in the first step of this work, we devised a simple and movable measuring system for the field condition by our own idea, and then we began to investigate the relationship between LPS and grain yield in rice varieties covering from old era to the present time. To get the answer for the question if the improvement of LPS can contribute to the increase of grain yield in rice.

The varieties used in this work were 32 varieties which were bred in Honshu island of Japan in the last 100 years, and they are genetically related with one another as shown in Fig.2. All the varieties were conventionally divided into three groups by the released year, as the old (bred in 1882–1913), the intermediate (bred in 1921–1940), and the new (bred in 1949–1976) groups. The eras when each group of the varieties were bred, corresponded to lst, 2nd, and 3rd stage respectively in Fig.1.

The seedlings of each variety, raised in the nursery bed by usual way, were transplanted at the spacing of 15x 30cm with a plant per hill, in the paddy field of the Experimental Farm of University of Tokyo. The plot for each variety was duplicated, and the size of a plot was 1.5x 8.0m. The compound fertilizer was applied at the

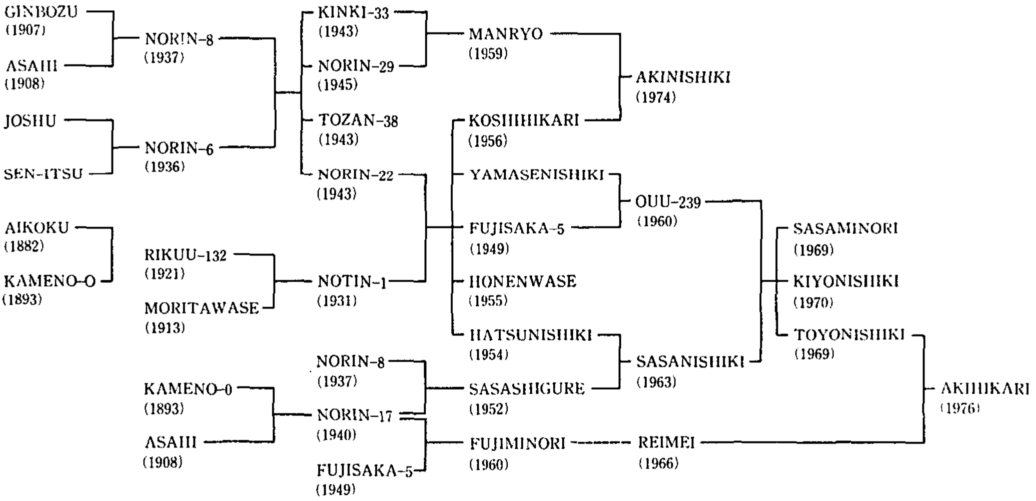

Fig. 2. Genetic relation of the rice varieties used in this paper. The figures in parenthesis are the year of release.

rate of 50, 75, and 50 kg/ha of N, P 205, and K 20 respectively as the basal dressing. In the top dressing plots, 50kg/ha of nitrogen as the form of ammonium sulfate was additionally applied at the heading time of each variety.

The measurement of photosynthesis was made on the canopy, and on the single leaf levels. An infrared CO_2 gas analyzer (Fuji Electric Co., Japan), a humidity sensor (VISALA, Sweden), and related facilities were installed in a van-type car, which made the measuring system movable on the level of the paddy field. The chamber for the canopy or for the single leaf was extended by teflon tubing from the car to the measuring spot.

CPS was measured in a closed system with 8 plants covered by an acrylic resin chamber (60 x 60 x 150 cm). The value of CPS was calculated from the initial decreasing rate of CO_2 concentration in the system obtained immediately after the system was changed to the closed one. Net time for one measurement was about 2 minutes, with about 5 more minutes for moving the chamber to the next measuring spot.

LPS and transpiration were measured simultaneously in the open system with a leaf mounted in an acrylic resin leaf chamber (1.5 x 10 x 0.3 cm). About 3 minutes was required for one measurement including the time for changing the leaf. The measurement of LPS was conducted in the vegetative stage (at the maximum tillering time) for the uppermost fully expanded leaf, and in the reproductive stage (at the heading, ripening, and harvesting times) for the flag leaf. Therfore, LPS in the vegetative stage and at the heading stage shows the potential capability of LPS for each leaf, and other LPS shows the values of the flag leaves in the senescing process. All the measurements of CPS and LPS were carried out under full sunlight.

The determination of grain yield was made for 9 plants in each plot, and the yield was expressed as the brown rice yield.

VARIETAL DIFFERENCE OF CANOPY PHOTOSYNTHESIS(CPS)

Table 1 shows the varietal differences of CPS and its components at the heading stage. The CPS components are usually considered to consist of LPS, leaf area index (LAI), and light intercepting efficiency which is conventionally indicated as the inclination angle of the flag leaf here. The highest mean value of CPS was found in the new varieties group, and furthermore, the number of the varieties which showed the value more than $4gCO_2/m^2/h$ was also the most in the new varieties group, indicating that the varietal improvement by breeding has been realized in respect of CPS.

Table 1. CPS, LPS, leaf area index, and flag leaf inclination of the varieties at the heading time

VARIETY	CPS ($gCO_2/m^2/h$)	LPS ($mgCO_2/dm^2/h$)	LAI (m^2/m^2)	ANG (deq.)
AIKOKU	2.91	41.1	2.63	25
KAMENO-O	2.62	31.6	4.03	28
GINBOUZU	3.71	35.6	3.67	17
ASAHI	3.31	33.2		27
MORITA-WASE	3.90	44.2	2.31	15
JOUUSHUU	3.33	42.8	3.92	22
SEN-ITSU	2.22	39.3	3.37	15
MEAN	3.14	38.3	3.32	21
RIKUU 132	4.76	36.7	3.58	25
TOUZAN 38	3.85	36.8	3.14	17
KINKI 33	3.42	35.4	3.59	13
FUJISAKA 5	3.76	43.5	2.88	17
NORIN 1	2.85	43.3	3.05	17
NORIN 6	3.33	36.1	3.14	10
NORIN 8	3.65	37.3	4.31	18
NORIN 17	4.79	39.6	3.11	12
NORIN 22	2.88	40.1	3.47	18
NORIN 29	3.39	36.0	5.03	10
MEAN	3.67	38.5	3.53	16
HOUNEN-WASE	3.48	41.6	3.80	12
KOSHIHIKARI	3.62	34.6	2.93	15
MANRYOU	4.93	40.0	3.50	13
FUJIMINORI	4.36	37.2	3.13	3
NIPPONBARE	2.76	36.1	3.72	7
SASANISHIKI	4.10	32.9	3.16	13
REIMEI	2.74	42.0	2.70	3
TOYONISHIKI	4.25	38.9	3.19	8
KIYONISHIKI	4.45	41.7	3.14	13
AKIHIKARI	4.73	40.1	3.25	13
HATSUNISHIKI	4.22	43.0	2.91	15
SASASHIGURE	3.65	31.9	3.45	12
AKINISHIKI	3.73	45.6	3.51	18
Oou-239	3.93	40.5	3.54	17
SASAMINORI		41.4	3.10	20
MEAN	3.93	39.2	3.27	12

As to the components of CPS, a significant differences could not be found in LPS and in LAI between three groups of the variety, but for the leaf inclination, we observed a clear trend of the flag leaves getting more erect with the change from old to new varieties. Therefore, it could be considered that the varietal difference of CPS was mainly attributed to the difference of light intercepting efficiency. Trenbath and Angus (1975) reported in the review of the relatioship between the leaf inclination and crop productivity, that the effect of leaf erectiveness is particularly large in rice, with the arguement being still conflicting in other crop species. The leaf inclination will get to play greater role with the increase of LAI. In this work, where LAI cannot reach high level, because the plants were transplanted with a plant per a hill, the effect of the leaf inclination is less appreciated.

VARIETAL DIFFERENCE OF THE SINGLE LEAF PHOTOSYNTHESIS (LPS)

It is known that there is a comparatively large diurnal change in LPS in the field condition. If that is too large, the values of LPS measured in the same day cannot be mutually compared. Therefore, we checked the magnitude of diurnal fluctuation of LPS as the preliminary experiment. As shown in Fig. 3, LPS showed an plateau from around 9 : 00 to 14 : 00. So, we decided to measure LPS during this 5 hours, which was long enough to process 32 varieties with our measuring system.

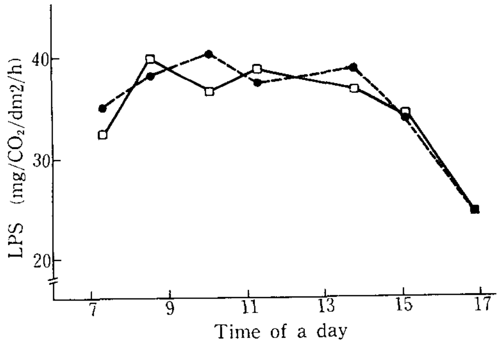

Fig. 3. Diurnal change of LPS
□—□; Akihikari, ●---●; Nourin 1

Table 2 shows LPS of a flag leaf in 32 varieties at the heading, ripening (2 weeks after the heading), and harvesting time. Since the maximum LPS of the flag leaf in each variety was observed at the heading time, we defined the LPS at this stage as the potential LPS of each variety. As clearly seen in Table 2, there is no significant difference in the potential LPS between these three groups. However, the LPS at the ripening stage, when the flag leaves are in the senescing process, showed an evident difference between the groups, with an incresing trend from old to new group of variety. Especially in the nitrogen top

Table 2. LPS of the varieties at heading, ripening, and harvesting stages (1985)

Variety	Heading	Ripening		Harvesting	
		Standard	Top-dress	Standard	Top-dress
Aikoku	41.1	38.1	42.6	17.4	16.7
Kamenoo	31.6	16.3	18.6	15.0	16.3
Ginbouzu	35.6	29.7	29.7	20.6	19.9
Asahi	33.2	25.4	24.6	26.8	23.3
Moritawase	44.2	25.1	26.7	22.1	17.0
Jyousyuu	42.8	25.5	21.1	18.6	19.2
Sen'itu	39.3	31.5	29.2	25.5	25 1
Old-Ave.	38.3	27.4	27.5	20.9	19.6
Rikuu-132	36.7	27.0	35.3	11.5	15.8
Touzan-38	36.8	30.8	34.2	17.1	17.1
Kinki-33	35.4	27.9	29.2	21.7	23.8
Fujisaka-5	43.5	25.7	31.5	18.5	21.4
Nourin-1	43.3	33.3	32.6	18.3	17.6
Nourin-6	36.1	22.8	29.9	17.8	22.8
Nourin-8	37.3	29.2	33.8	22.9	22.6
Nourin-17	39.6	30.9	38.8	14.5	16.5
Nourin-22	40.1	28.2	33.1	20.3	25.2
Nourin-29	36.0	33.3	32.3	27.9	30.2
Mid-Ave.	38.5	28.9	33.1	19.1	21.3
Hounenwase	41.6	33.5	41.0	24.8	21.4
Kosihikari	34.6	30.4	33.9	14.1	16.0
Manryou	40.0	39.2	46.6	21.9	25.7
Fujiminori	37.2	29.3	30.9	15.4	16.4
Nipponbare	36.1	28.2	36.3	19.9	19.0
Sasanisiki	32.9	27.9	36.6	22.1	19.0
Reimei	42.0	30.8	31.3	18.6	18.9
Toyonisiki	38.9	29.5	40.9	18.7	20.0
Kiyonisiki	41.7	26.8	28.5	14.9	15.9
Akihikari	40.1	35.2	34.0	15.3	18.1
Hatunisiki	43.0	30.1	35.5	20.2	21.1
Sasasigure	31.9	31.3	35.9	19.6	22.0
Akinisiki	45.6	30.8	38.7	27.7	28.3
Oou-239	40.5	31.6	37.0	20.7	24.0
Sasaminori	41.4	35.1	36.7	21.0	22.9
New-Ave.	39.2	31.3	36.3	19.7	20.6

Standard : no dressing of nitrogen, Top-dress: top dressing of nitrogen at the heading time.
The values are expressed in $mgCO_2/h$.

-dressed plots, the varietal difference was large. this would be due to the different responsiveness of LPS to increased nitrogen level ; no response in the old varieties group, and large response in the new varieties group. At the harvesting time the varietal difference in LPS practically disappeared again.

Adding the data of LPS at the vegetative (maximum tillering) stage, which can be considered to be also the potential LPS because that was measured on the just fully expanded leaves the correlation coefficients of LPS between different growth stages were calculated to know the stability of LPS values of the variety (Table 3). A significant correlation was found between vegetative and heading stages, with no correlation between any combination of the stages. This means that the potential LPS shown in the young leaves are stable irrespective of the growth stages, and further means that there is no mutual *relation between the potential LPS and the LPS in* the senescing leaves. To examine further the stability of LPS value, we calculated the correlation coefficients of LPS between three successive years, 1984, 1985 and 1986 (Table 4). As potential LPS of young leaves are stable through the different years.

Table 3. Correlation coefficients between LPS at different growth stages

Stage	Heading	Ripening	Harvesting
Vegetative	.694**	.278	-.016
Heading	—	.323	.099
Ripening	—	—	.192

Table 4. Correlation coefficients between LPS in different years

Stage	Vegetative	Heading	Ripening	Harvesting
1984-1985	—	.474**	.187	.297
1984-1986	—	.438*	.312	—
1985-1986	.498**	.500**	.125	—

These data would suggest that the potential LPS is stable, but the LPS in the senescing *predicted from the above result*, the significant correlation was found in the LPS of the vegetative and heading stages, *suggesting that the* process is not stable through the different growth stages and different years. Consequently, the potential LPS can be considered to be specific to the variety, *although LPS in the senescing process* is not variety specific.

In the next step, we investigated the mechanism of the varietal difference of LPS, from the viewpoint of CO_2 diffusion resistances. LPS is *determined by two processes, the magnitude of* which can be expressed by stomatal (rs), and mesophyll (rm) diffusion resistances. Table 5 shows correlation coefficients between LPS and rs or rm at each growth stage. LPS correlates more *strongly with rm, suggesting that* CO_2 diffusive process in the leaf tissue and CO_2 fixation process in the chloroplasts contribute more to the varietal difference of LPS, especially in the ripening and harvesting stages.

Table 5. Correlation coefficients between LPS and rs or rm at different growth stages

	Vegetative	Heading	Ripening	Harvesting
LPS-rs	-.671**	-.545**	-.207	-.095
LPS-rm	-.944**	-.683**	-.897**	-.923**

RELATIONSHIP BETWEEN LPS AND GRAIN YIELD

It was a main objective in this work to know if there is a correlation between LPS and grain yield. We could find a significant positive correlation between LPS and grain yield only at the ripening stage in nitrogen top-dressed plots, with the rather negative correlation at the heading stage (Fig.4 and 5). This shows that the potential capability of LPS has no relation with the grain yield, but that in the grain filling period has comparatively close relation. The positive correlation at the ripening stage is related to the fact that LPS at the grain filling time showed a high correlation (r=0.54**) against the release year of variety as shown in Fig 6, suggesting that the improvement of LPS surely took place in the course of breeding for high yielding variety.

From the results of this work, we can say that

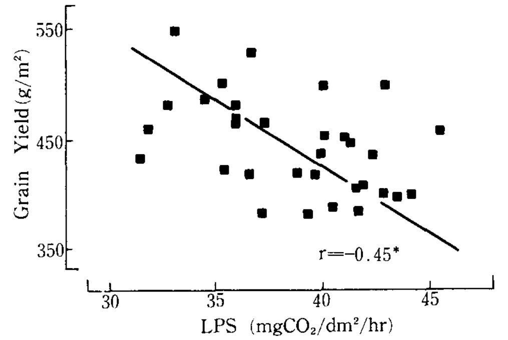

Fig. 4. Relationship between LPS at heading stage and grain yield

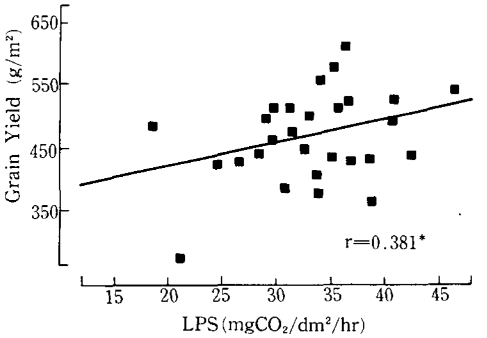

Fig. 5. Relationship between LPS at ripening stage and grain yield

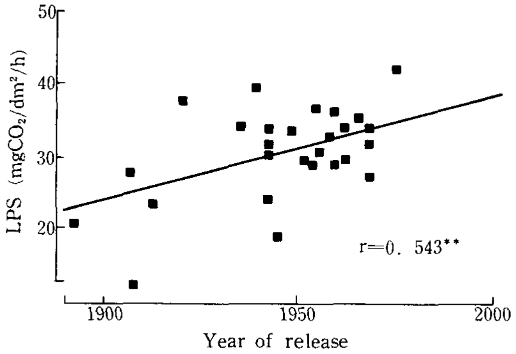

Fig. 6. Change of LPS at the ripening stage with the progress of year of release

the genetic improvement of LPS in the ripening stage at least, can contribute to the increase of the grain yield of rice, although the potential LPS cannot. So, high LPS at the ripening stage can be the breeding objective for high yielding varieties. However, the problem is that LPS in the ripening stage is not stable. That means LPS in this stage is easily influenced by the climate condition of every year. Therefore, our efforts should be concentrated to making the varieties with great stability of LPS against the climatic variation, as well as the varieties with basically high LPS and slow progress of senescence.

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