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PLANT FACTORS RELATED TO DRY MATTER PRODUCTION IN RICE CULTIVARS

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ABSTRACT

In order to clarify cultivar differences in dry matter production during the reproductive and grain filling periods (DMP_{RP} and DMP_{GF}) and to investigate their related factors, rice experimental data are discussed in this paper. Ten rice cultivars were grown on a paddy field at Kyoto University in 2001, under optimum nutrient supply (12 g m^{-2} N, 12 g m^{-2} P_2O_5 and 12 g m^{-2} K_2O). Radiation use efficiency (RUE) during the reproductive and grain filling period (RUE_{RP} and RUE_{GF}) had significant positive correlations with DMP during reproductive and grain filling periods (DMP_{RP} and DMP_{GF}). Crop Growth Rate (CGR) had also significant positive correlations with RUE_{RP} and RUE_{GF}, and they were much closer than that between CGR and Leaf Area Index (LAI), indicating that variation among cultivars in DMP_{RP} and DMP_{GF} were more related to that in RUE rather than variation in light interception trait of the crop. RUE_{RP} and RUE_{GF} were more associated with Single Leaf Photosynthetic Capacity (Pn) than with Light Extinction Coefficient (k) during reproductive and grain filling period, and it was also associated with panicle depth during grain filling period. Pn during reproductive and grain filling period had close positive correlations with Leaf Stomatal Conductance (Gs) during respective periods, and had no significant correlation with N content per leaf area. In conclusion, a major part of variation among cultivars in DMP was caused by RUE for both the reproductive and grain filling phase. Photosynthetic activity of single leaf was a dominant contributor to RUE, and it was primarily determined by stomatal conductance.

Key words: light extinction coefficient, radiation use efficiency, reproductive and grain filling period, single leaf photosynthetic capacity

INTRODUCTION

In a previous paper it was shown that dry matter production during the grain filling period (DMP_{GF}) had a consistently higher contribution to the yield variation among cultivars than the other source component, non-structural carbohydrate (NSC) pre-reserved at full heading (Lubis *et al*., 2003). In addition, sink formation and NSC accumulation up to full heading that seemed largely and potentially involved in genotypic variation in yield, respectively, also varied among cultivars responding DMP during the reproductive period (DMP_{RP}) through crop growth rate (CGR) during the late reproductive period (Horie, 2001; Horie *et al*., 2002; Wada, 1969). This paper will observe the major factors that caused genotypic variation in DMP_{GF} and $DMP_{RP.}$

A number of studies had focused on crop photosynthesis to explain cultivar differences in dry matter productivity. Light distribution in the canopy would be possible as one of important factors (Long *et al*., 2006). Laza *et al.* (2004) argued the importance of light distribution for dry matter production, especially during grain filling. Taylaran *et al.* (2009) reported that higher DMP_{GF} of new cultivars than old ones was related to smaller light extinct tion coefficient in new cultivars. Based on the analysis with a crop photosynthesis model, Mesgaran *et al.* (2006) attributed a part of difference in dry matter productivity observed among cultivars to their difference in light extinction coefficient.

Leaf photosynthetic ability also has been proposed to bring about variation in DMP among rice genotypes. Saitoh *et al.* (1991) observed higher maximum photosynthesis rate (Pn) of upper most leaves in a high yielding indica-japonica hybrid than a japonica rice. Comparing old and modern Japanese cultivars, Saitoh *et al.* (1993) observed relatively well-maintained Pn with progress of grain filling in modern and better yielding cultivars. Kuroda and Kumura (1990a) also compared old and new cultivars in Japan found that single leaf photosynthesis was clearly higher in the new cultivars at grain filling, although at heading there was no or little difference in Pn between the two groups.

Nitrogen nutrition is frequently mentioned as a determinant factor for photosynthetic ability of single leaf (Taylaran *et al.*, 2011), and nitrogen content in the leaf had high correlation with the SPAD value (Islam *et al.*, 2009). Kawamitsu and Agata (1987), using 50 divergent cultivars grown under a controlled condition, observed a close correlation between photosynthetic rate and leaf or mesophyll conductance and found, although loose, there was a correlation between Pn and leaf N content. However, Kuroda and Kumura (1990b) showed that new rice varieties had higher Pn than did old varieties with the same nitrogen content of the leaf. Sasaki and Ishii (1992) reported that cultivar difference in Pn of flag leaf was closely associated with mesophyll conductance to CO_2 and stomatal conductance was associated with cultivar difference in Pn, but it was true at relatively limited stages.

In view of the above findings, variation in Pn among rice cultivars has been repeatedly observed in the field, but the traits to cause varied activity are not necessary clear. In addition, due to limitation of direct observations, it needs further investigation to determine if Pn contributes to genotypic variation in rice DMP and yielding ability. Also, information on relative importance of Pn and the trait of canopy structure is very limited.

DMP during a period is a product of cumulative intercepted radiation during the period and radiation use efficiency (RUE), which has been suggested fairly constant in rice crop over most growth period and independent of the weather conditions (Horie and Sakuratani, 1985). Thus leaf area index (LAI) and its duration should be the first crop factor to determine DMP affecting the sum of radiation interception. RUE then would be related to canopy structure and/or leaf photosynthetic activity. In this paper, the variation among cultivars in DMP_{GF} and DMP_{RP} was investigated in relation to LAI, light extinction coefficient, photosynthesis and panicle depth.

MATERIALS AND METHODS

Analyses were based on experimental results of 10 rice cultivars of a wide range of genotypes from a local cultivar of tropical japonica to an indica of the new plant type bred by IRRI. Rice cultivars that potentially have high yield from different countries and one tropical japonica as comparator (Table 1.) were grown in a paddy field at Kyoto University in 2001, latitude 35.0°N, longitude 135°E with an elevation of 20 m from the sea level. The soil type is classified as alluvial sandy loam and gray lowland soil (Haplaquept) with 3.1 and 0.22 % of total carbon and nitrogen (N) contents, respectively (unpublished data). The experiment was arranged in a randomized block design with three replications. The planting date was May 25, and plant spacing was 30 cm x 15 cm with one plant per hill. Fertilizers (12 g m^{-2} N, 12 g m^{-2} P_2O_5 and 12 g m^{-2} K_2O) were applied for all cultivars. Nitrogen was applied in five splits, and P_2O_5 and K_2O applied as basal. Aboveground crop dry weight was measured at mid tillering, panicle initiation, 2 weeks before full heading, full heading, 2 weeks after full heading and maturity stage for determination of dry weight after being oven dried at 80^{o}C for 48 hours. Nitrogen content was determined for the sampled materials with a near infrared reflectance analyzer (Bran + Luebbe InfraAlyzer 500), and for calibration, it was measured by the Kjeldahl method.

Leaf photosynthesis and stomatal conductance were measured by LICOR LI-6400 for the uppermost fully expanded leaves at three to five times for each of the four periods, panicle initiation (PI) to two weeks before heading (2wBH), 2wBH to full heading (FHD), FHD to two weeks after full heading (2wAH) and 2wAH to maturity (M). The measurement was conducted under higher PAR intensity than 1200 µmol m^{-2} s^{-1} between 9.00 a.m to 1.00 p.m for three leaves of every cultivar in each of the three replications.

Light extinction coefficient (k) of diffused radiation in the crop canopy was determined by the method of stratified leaf harvesting when that almost light is consisted of diffuse radiation (PAR < 500 µmol m^{-2} sec^{-1}). This measurement was conducted twice at late reproductive and early grain filling stages. The intensity of PAR at the center of four plants was measured at each layer, using an aluminum stick as gauge and by ACCU PAR, Decagon. The depth of first layer was 15 cm for late reproductive and 30 cm for early grain filling measurements from the top of the canopy and the interval of below was 15 cm up to the fourth layer. Two plants of measurement site were harvested, then area of leaf and panicle, if exists, of each layer were determined and their dry weight was measured. The panicle area here means the shadow area projected by panicle when it is naturally spread down on the horizontal sheet. Light extinction coefficient, k, was derived with the equation,

$$I/Io = \exp(-k\ F)$$

where, I/Io is relative intensity of PAR at a layer and F is cumulative LAI from the top of the canopy up to the layer.

A single value of k was determined for each canopy by the linear regression between ln(I/Io) and F. To take into account the shade by panicle in the canopy, the area of panicle in each layer was added to the respective leaf area and the calculated value of light extinction coefficient was designated as k*.

RUE was determined for the periods of early and late reproductive growth and early and late grain filling by dividing DMP with cumulative of daily intercepted radiation (S) and exponential of light extinction coefficient (k) and leaf area index (LAI), as expressed below:

$$RUE = DMP/[S\{1-\exp(-k\ LAI)\}]$$

RESULTS AND DISCUSSION

Variation in Dry Matter Production during Grain Filling

Grain yield (0% moisture) ranged from 408 g m^{-2} of Banten to 895 g m^{-2} of Takanari. DMP_{RP} ranged from 521 g m^{-2} of Banten to 828 g m^{-2} of Takanari and DMP_{GF} ranged from 243 g m^{-2} of Banten to 669 g m^{-2} of Takanari (Table 1). Takanari had the highest Grain Yield, DMP_{RP} and DMP_{GF} among cultivars, and Banten always had the lowest.

Table 1. Type and origin country of rice cultivars used in the experiment and their grain yield and dry matter production.

Cultivar	**Type**	**Country Origin**	**Grain**	**DMP_{GF}** g m^{-2}	**DMP_{RP}**
Takanari	Indica x Japonica	Japan	895	669	828
Shanguichao	Indica	China	805	603	715
IR72	Indica	Philippines	782	575	771
Nipponbare	Japonica	Japan	666	554	556
Takenari	Japonica	Japan	607	423	738
NPT	Indica x Tropical Japonica	Philippines	605	448	734
Koshihikari	Japonica	Japan	595	518	656
WAB	*Glaberrima* x *Sativa*	Coted`Ivoire	513	317	610
Ch86	Indica	China	421	292	806
Banten	Tropical Japonica	Indonesia	408	243	521

NPT = IR65564-44-2-2 and WAB = WAB450-1-B-P-38-HB. DMP_{RP} and DMP_{GF} are dry matter production during reproductive and grain filling period, respectively.

Relations among Dry Matter Production, Crop Growth Rate and Radiation Use Efficiency

Dry Matter Production (DMP) is determined by crop growth rate (CGR) during respective period, and CGR is the product of daily intercepted radiation and radiation use efficiency (RUE).

CGR had significantly positive correlation with RUE during reproductive and grain filling period and it was much closer than the relationship between CGR and LAI (Table 2). These results indicated that the variation of DMP_{RP} and DMP_{GF} are associated primarily with RUE during the respective periods.

Table 2. Correlation coefficient of CGR with RUE and LAI during reproductive and grain filling period for 10 cultivars.

	CGR during Reproductive Period				**CGR during Grain Filling Period**		
	Early	**Late**	**Mean**		**Early**	**Late**	**Mean**
RUE	0.57+	0.78**	0.74**	RUE	0.89***	0.87***	0.81**
LAI	0.39ns	0.31ns	0.42ns	LAI	-0.29ns	0.84**	0.63*

ns, +, *, ** and *** denote not significance and significance at 10%, 5%, 1% and 0.1% levels, respectively.

The variation in CGR was not associated with the amount of intercepted radiation but with RUE. These facts further indicated that the variation among cultivars in DMP correlated with variations in mean RUE during reproductive and grain filling period.

RUE and its Related Factors

Mean RUE during reproductive period ranged from 1.33 g MJ^{-1} of Nipponbare to 1.73 g MJ^{-1} of Shanguichao (Table 3), and mean RUE during grain filling period ranged from 0.86 g MJ^{-1} of Ch86 to 1.51 g MJ^{-1} of Koshihikari (Table 4).

Seasonal pattern of Single leaf photosynthesis (Pn) showed higher values during reproductive period and declined during grain filling (Figs. 1). Takanari had almost the highest Pn in almost all of growth periods. Mean Pn during reproductive period was differed among cultivars, and it ranged from 20.4 µmol m^{-2} sec^{-1} of Takenari to 27.7 µmol m^{-2} sec^{-1} of Shanguichao (Table 3). During grain filling period it ranged from 15.4 µmol m^{-2} sec^{-1} of Takenari to 20.8 µmol m^{-2} sec^{-1} of Takanari (Table 4).

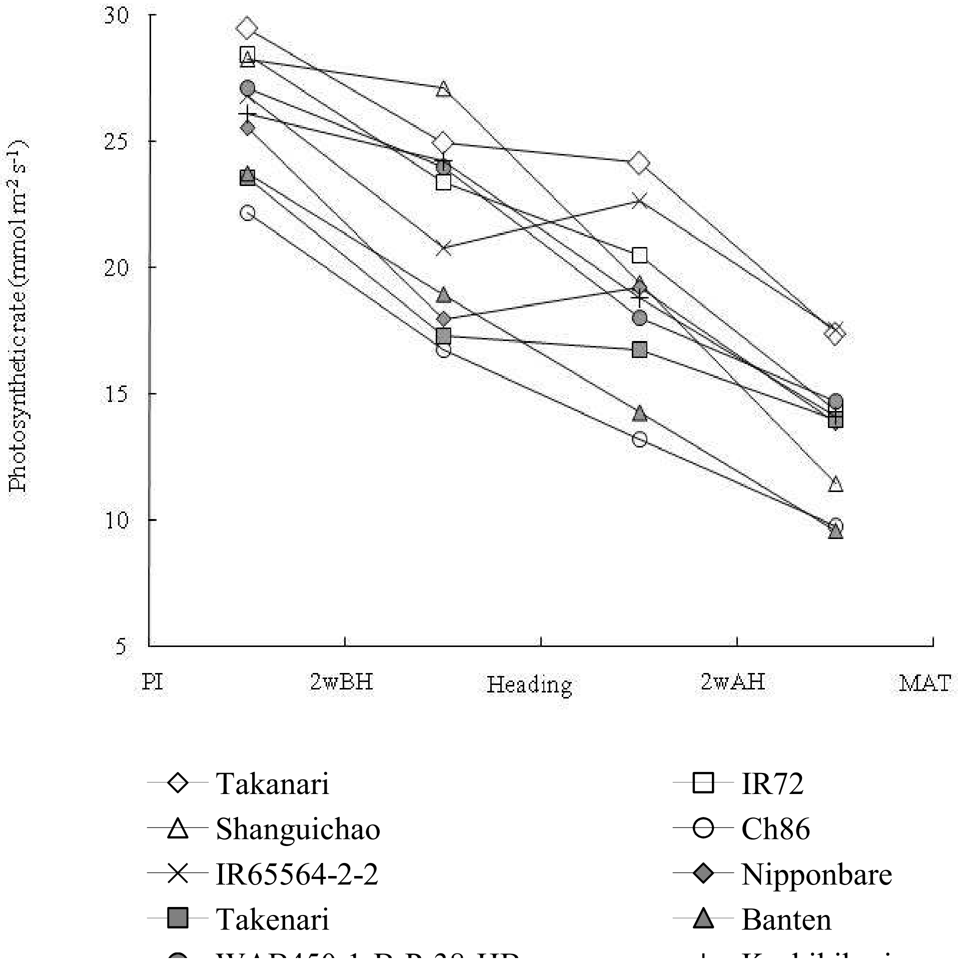

Fig. 1. Seasonal pattern of single leaf photosynthesis (Pn) of rice cultivars.

Light extinction coefficient (k) ranged from 0.34 of Takenari to 0.55 of Koshihikari at late reproductive period, while at early grain filling it ranged from 0.53 of Koshihikari to 0.70 of Takenari (Table 3 and 4). If we consider light interception by panicle in the canopy, the light extinction coefficient that includes panicle area (k*) was smaller than k, and it ranged from 0.51 of Koshihikari to 0.67 of Takenari. The stratified harvesting of panicle along with leaves allowed calculation of the mean depth of panicle in the canopy as expressed by leaf area index above the mid point of the horizontal profile of panicle area (Table 4). A large variation of panicle depth was observed ranging from 0.1 of Nipponbare to 2.37 of NPT.

Table 3. CGR, RUE and related factors during reproductive period for 10 cultivars.

Cultivar	**CGR**	**RUE**			**LAI**		
	Mean	**Early**	**Late**	**Mean**	**Early**	**Late**	**Mean**
	g m^{-2} d^{-1}	--------	g MJ^{-1}	------	---------	------	--------
Takanari	22.9	1.62	1.74	1.68	5.11	5.63	5.37
IR72	21.5	1.53	1.57	1.55	5.80	7.00	6.40
Shanguichao	24.0	2.01	1.45	1.73	5.72	6.85	6.28
Nipponbare	17.9	1.16	1.50	1.33	5.88	6.53	6.20
Takenari	20.3	1.69	1.40	1.55	5.53	6.50	6.01
NPT	18.5	1.45	1.37	1.41	5.04	6.19	5.61
Koshihikari	21.8	1.53	1.45	1.49	3.63	4.80	4.22
WAB	17.8	1.59	1.28	1.44	3.68	4.21	3.95
Ch86	22.9	2.00	1.42	1.71	4.92	5.56	5.24
Banten	13.1	1.86	0.96	1.41	4.15	3.85	4.00
Mean	20.1	1.65	1.42	1.53	4.94	5.71	5.33
STD	3.3	0.26	0.20	0.14	0.85	1.11	0.96

Cultivar	**K**	**Pn**		
	Late	**Early t**	**Late t**	**Mean**
	-	-------	µmol m^{-2} sec^{-1}	-------
Takanari	0.40	29.5	24.9	27.2
IR72	0.40	28.4	23.4	25.9
Shanguichao	0.35	28.3	27.1	27.7
Nipponbare	0.36	25.5	18.0	21.7
Takenari	0.34	23.6	17.3	20.4
NPT	0.40	26.8	20.8	23.8
Koshihikari	0.55	26.1	24.2	25.2
WAB	0.43	27.1	24.0	25.6
Ch86	0.68	22.2	16.8	19.5
Banten	0.43	23.7	18.9	21.3
Mean	0.43	26.11	21.53	23.82
STD	0.10	2.37	3.65	2.91

t The average of (3-5) measurements during early reproductive period (panicle initiation to 15 days after panicle initiation) and (3-5) measurements during late reproductive period (15 days after panicle initiation to full heading stage).

Table 4. CGR, RUE and related factors during grain filling period for 10 cultivars.

Cultivar	**CGR Mean, g m^{-2} d^{-1}**	**RUE,** g MJ^{-1}			**LAI**		
		Early	**Late**	**Mean**	**Early**	**Late**	**Mean**
Takanari	18.8	1.52	1.39	1.46	5.46	3.02	4.24
IR72	14.6	1.09	1.23	1.16	6.44	5.11	5.77
Shanguichao	11.5	0.90	1.33	1.11	6.09	5.10	5.59
Nipponbare	14.1	1.08	1,24	1.16	6.13	5.17	5.65
Takenari	13.0	1.03	0.91	0.97	5.80	4.24	5.02
NPT	13.4	1.14	1.08	1.11	5.57	4.80	5.19
Koshihikari	20.8	1.62	1.40	1.51	4.64	3.52	4.08
WAB	13.1	1.10	0.93	1.01	3.64	2.94	3.29
Ch86	10.1	1.38	0.33	0.86	4.86	2.91	3.89
Banten	9.0	1.66	0.30	0.98	2.92	1.81	2.36
Mean	13.8	1.25	1.02	1.13	5.15	3.86	4.51
STD	3.6	0.27	0.41	0.21	1.15	1.18	1.13

Cultivar	**k**	**k* t**	**Pn**			**Panicle tt**	**Mean ttt**
	Early	**Early**	**Early #**	**Late #** µmol m^{-2} sec^{-1}	**Mean**	**Area Index Early**	**depth of Panicle in LAI**
	-	-	--------		-------	--------	m m^{-2}
Takanari	0,57	0,54	24,1	17,4	20,8	0,97	1,12
IR72	0,64	0,60	20,5	14,3	17,4	1,10	1,48
Shanguichao	0,63	0,58	19,4	11,4	15,4	1,02	0,86
Nipponbare	0,58	0,56	19,2	13,9	16,5	0,61	0,10
Takenari	0,70	0,67	16,7	14,0	15,4	0,77	0,33
NPT	0,56	0,53	22,7	17,6	20,1	0,78	2,37
Koshihikari	0,53	0,51	18,8	14,1	16,5	0,69	0,68
WAB	0,61	0,52	18,0	14,7	16,3	0,55	1,20
Ch86	-	-	13,2	9,8	11,5	-	-
Banten	0,68	0,63	14,3	9,6	11,9	0,59	0,80
Mean	0,61	0,57	18,69	13,67	16,18	0,79	0,99
STD	0,06	0,05	3,40	2,74	2,98	0,20	0,67

t The area of panicle was added to the respective of leaf area in calculation of light extinction coefficient,
tt panicle area per land area, and ttt area of leaf in the mean depth of panicle.

The average of (3-5) measurements during early grain filling period (full heading to 15 days after full heading) and (3-5) measurements during late grain filling period (15 days after full heading to maturity).

The correlation coefficients between mean RUE and Pn were significant during late reproductive (r = 0.58+) and mean grain filling periods (r = 0.65*), however there were no significant correlation for other periods. (Table 5). Although there were no significant correlation between k and RUE in most of growth periods, there was a negative correlation tendency between k and RUE during mean grain filling period (r = -0.65+). Correlation between k* and RUE during early grain filling period showed negative value, however it were not significant for all of grain filling periods. In view of the mean values of the reproductive and grain filling periods, the correlation coefficient with RUE was greater for Pn than for k. The depth of panicle had no correlation with RUE in both the early and late grain filling periods (Table 5).

Table 5. Correlation coefficient of RUE with Pn and k during reproductive and also panicle depth during grain filling period for 10 cultivars.

	RUE during reproductive Period				**RUE during Grain Filling Period#**		
	Early	**Late**	**Mean**		**Early**	**Late**	**Mean**
Pn	-0.26ns	0.58+	0.33ns	Pn	-0.18ns	0.45ns	0.65*
k	0.34ns	-0.18ns	0.15ns	k	-0.25ns	-0.37ns	-0.65+
				k*	-0.15ns	-0.28ns	-0.45ns
				Panicle Depth	-0.002ns	0.026ns	0.029ns

Pn during reproductive period had a significantly positive correlation with Gs, and had no correlation with N content per leaf area during that period. The similar result was observed during grain filling period, in which Pn had a notably close correlation with Gs but had no correlation with leaf N content per leaf area. There was also no correlation between leaf stomatal conductance and nitrogen content per leaf area during reproductive period as well as during grain filling period (Table 6). These facts indicated that single leaf photosynthesis (Pn) mostly determined by stomatal conductance (Gs) during growth of rice.

Table 6. Correlation coefficient among leaf photosynthesis, leaf stomatal conductance and N content per leaf area during reproductive and grain filling period.

Traits	**Reproductive Period**			**Grain Filling Period**		
	Early	**Late**	**Mean**	**Early**	**Late**	**Mean**
Pn vs Gs	0.85**	0.69+	0.75*	0.89**	0.82**	0.86**
Pn vs N	0.19ns	-0.38ns	-0.01ns	-0.05ns	-0.25ns	-0.12ns
Gs vs N	0.21ns	-0.31ns	0.07ns	-0.22ns	-0.19ns	-0.17ns

RUE represents the efficiency to produce dry matter with unit amount of solar energy the crop received and basically reflects photosynthetic capacity of the crop. Thus RUE would be supported by the ability of single leaf photosynthesis and canopy architecture. In this study, variation among cultivars in Pn tended to positively associate with that of RUE, although it was not quite distinct during grain filling period. On the other hand, k had no significant correlation with RUE during reproductive and grain filling period. The effect of panicle existence was examined by partial correlation between mean panicle depth and RUE, but no significant correlation was found. The absence of partial correlation between k and RUE might be due to the size of LAI of rice cultivars in this experiment that were exceeded 4.0 which was enough to intercept the radiation.

The depth of panicle should be in combination with the erect of panicle and higher single leaf photosynthetic ability that would be performed higher crop photosynthesis. Thus it is evident that Pn contributed to variation in RUE during grain filling period to greater extent than did k and panicle depth. Notably consistent result was obtained from two years for the cultivar difference in seasonal change of Pn. Takanari, with high RUE during the both reproductive and grain filling periods, always exhibited higher Pn than most of the others. This indicates that the high productivity of this cultivar would be attributable to high activity of leaf photosynthesis. Therefore, it is very likely that photosynthetic activity is an important determinant to cause genotypic variation in dry matter productivity for both DMP_{RP} and DMP_{GF}.

CONCLUSION

In conclusion, a major part of variation among cultivars in Dry Matter Production during the reproductive and grain filling periods was caused by Radiation Use Efficiency in the respective periods. Single Leaf Photosynthetic capacity supported high Radiation Use Efficiency apparently and Single Leaf Photosynthetic capacity is primarily determined by stomatal conductance.

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