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Physio-Morphological Characters of F_1 Hybrids of Rice (*Oryza sativa* L.) in Japonica-Indica Crosses

I. Heterosis for photosynthesis

Mohammad Abu Zaman Sarker, Seiichi Murayama*, Yukio Ishimine* and Eiji Tsuzuki**

(*United Graduate School of Agricultural Sciences, Kagoshima University, Kagoshima 890-0065, Japan;*
**Faculty of Agriculture, University of the Ryukyus, Nishihara, Okinawa 903-0213, Japan;*
***Faculty of Agriculture, Miyazaki University, Miyazaki 889-2192, Japan*)

Abstract: A pot experiment was conducted to study photosynthetic rate in terms of carbon dioxide exchange rate (CER), chlorophyll meter reading (SPAD value) and specific leaf area (SLA) of 12 F_1 hybrids from crosses between japonica and indica rice and their parents, and to estimate the heterosis in F_1 hybrids at active tillering, flowering and dough ripe stages. In all F_1 hybrids and parent cultivars, CER was high at the active tillering stage with a small heterosis value. A positive heterosis for this trait was found at the flowering stage. The magnitude of heterosis for CER depended on the cross combinations. Although a positive heterosis for SPAD value was found at the active tillering stage, there was no correlation between heterosis for SPAD value and that for CER at the flowering stage, at which heterosis for CER was positive. Heterosis for SLA was high at the active tillering stage and gradually decreased thereafter. Heterosis for CER might be dependent not only on negative heterosis for SLA but also on other photosynthetic factors such as N content, soluble protein content and Rubisco activity.

Key words: F_1 hybrid, Heterosis, Photosynthetic rate, SLA, SPAD value.

The phenomenon of heterosis has been clearly demonstrated in rice. This heterosis can be expressed in agronomic, physiological and biochemical traits. F_1 hybrids in rice have gained increased attention by rice breeders and agronomists after its successful introduction commercially in China and the Democratic People's Republic of Korea (Virmani, 1994). Recently, commercialization of F_1 hybrid rice has been initiated in India, Vietnam and the Philippines (Virmani, 1996).

Although the advantage of F_1 hybrid rice in dry matter production and other characters associated with the yield potential has been identified, the physiological basis for this heterosis is not well documented (Peng et al., 1999). Heterosis for photosynthesis, the most fundamental physiological reaction for plant growth, has been investigated to identify the physiological characteristics responsible for vigorous growth and/or increased dry matter production in F_1 hybrids, but consistent results have not been obtained (Akita, 1988). However, McDonald et al. (1974) and Murayama et al. (1987) reported a high positive heterosis for photosynthesis and positive heterosis for nitrogen content in F_1 hybrids. Most of the studies in the past were made with indica-indica crosses or a few japonica-japonica crosses, and reports on inter-subspecific heterosis between japonica and indica are scanty. Kabaki (1993) found no differences in the photosynthetic activity between hybrid rice of japonica-indica and parents. However, it is also necessary to investigate other parameters related to photosynthesis at different growth stages.

The present study was undertaken to investigate the heterosis for photosynthesis, chlorophyll content and leaf thickness at different stages in japonica-indica F_1 hybrids.

Materials and Methods

The experiment was conducted in a glasshouse of the Faculty of Agriculture, University of the Ryukyus, Okinawa, Japan (26°10′ N and 127°45′ E). F_1 seeds were produced during the second season of 1998 using 4 japonica cultivars as female parent and 3 indica cultivars as male parent. The japonica cultivars were Murasaki Ine, Chiyonishiki, Suzunari and Akebono, and the indica cultivars were Dhaka, Dharial and Dular. These indica cultivars are generally cultivated in Aus season in Bangladesh.

The experiment was laid out in a completely randomized design. Seeds of 7 parent cultivars and 12 F_1 hybrids were treated with a systemic fungicide "Benlate" for 24 h and were incubated at 30°C for 48 h for germination. Pre-germinated seeds were sown on nursery boxes (60 × 35 × 8 cm) on 12 Feb. 1999. Twenty-eight-day-old seedlings (3-4 leaves) were transplanted into 0.02 m^2 Wagner pots containing Shimajiri Mahji (dark reddish) soil distributed in the Okinawa region. Organic matter "Minori" was added at the rate of 3 kg m^{-2} and a basal

Received 20 September 2000. Accepted 23 February 2001. Corresponding author : S. Murayama (smurayam@agr.u-ryukyu.ac.jp, fax +81-98-895-8749).

Abbreviations: CER, carbon dioxide exchange rate; DAT, days after transplanting; F_1, first filial generation; SLA, specific leaf area; SPAD, chlorophyll meter.

dose of chemical fertilizers N, P_2O_5 and K_2O was applied at the rate of 7.5, 12.0 and 9.6 g m^{-2}, respectively, one day before transplanting. The soil in the pots was puddled in order to simulate wetland paddy field conditions. First top dressing of N was applied at the rate of 2.9 g m^{-2} at 14 d after transplanting (DAT). An additional application of N was made also as a second top dressing at 28 DAT (at active tillering stage) at the rate of 2.9 g m^{-2} to minimize the possible shortage of N supply for photosynthetic process. Final top dressing of N and K_2O was applied at the rate of 4.5 and 4.2 g m^{-2}, respectively, at 43-59 DAT depending on the panicle initiation stage observed previously, i.e., 17-24 d before flowering (Table 1). The pots were watered daily. The glasshouse was well ventilated in order to maintain natural temperature fluctuations. The crop was kept free from mites and insects by applying Kelthane 40 EC and Diazinon 5 G, at 28 and 35 DAT, respectively.

The date of flowering was recorded by eye-estimation when about 50% of the plants started flowering. Carbon dioxide exchange rate (CER), chlorophyll meter reading (SPAD value) and specific leaf area (SLA) were measured 3 times during the growing period *viz.*, at active tillering, flowering (when 50% plants flowered) and dough ripe (12-13 d after flowering) stages. At the active tillering stage, CER of all the parents and F_1 hybrids was measured at 42 DAT; thereafter, that of only the F_1 and its parents of the cross combination in a day, when the flowering time varied less than 11 d. CER was measured using a portable infrared CO_2 gas analyzer (LCA-2, ADC Ltd., England) and Parkinson leaf chamber specially designed for grass leaves. Three halogen lamps of 500 W were used to maintain a light intensity of about 1200 μmol m^{-2} s^{-1} during the evaluation period. An atmospheric air flow rate of 400 mL min^{-1} inside the chamber was achieved using an Asu M-2 air supply unit. The chamber was maintained at 30±1°C during the measuring period.

Three plants for each parent cultivar or F_1 hybrid were selected randomly for CER measurement. Two Y-leaves (most recently matured leaf blades) (Ntamatungiro et al., 1999) or flag leaves from each plant, i.e., 6 leaves for each parent cultivar or F_1 hybrid were used and 3 readings were recorded from each leaf. SPAD readings were taken from the same parts of those 6 leaves just after CER measurement, using a leaf chlorophyll meter (SPAD 502, Minolta, Japan). At the following day, 5 plants from each parent cultivar or F_1 hybrid were sampled. Leaf blades were separated and the area was measured immediately with an automatic area meter (AAM-8, Hayashi Denkoh Co. Ltd., Japan). Dry matter of the leaf blades was measured after oven drying at 80°C to a constant weight. Specific leaf area (SLA) was calculated according to the following formula,

$$SLA = \frac{\text{Leaf area}}{\text{Leaf weight}}$$

Table 1. Date of final top dressing, days to flowering and heterosis for days to flowering in F_1 hybrids.

F_1 hybrid / parent	Date of final top dressing	Days to flowering[a]	Heterosis
Murasaki Ine × Dhaka	24 April (21)	64	0.98
Murasaki Ine × Dharial	10 May (20)	79	1.20
Murasaki Ine × Dular	24 April (19)	62	0.98
Chiyonishiki × Dhaka	30 April (19)	68	0.97
Chiyonishiki × Dharial	" (22)	71	1.00
Chiyonishiki × Dular	" (20)	69	1.01
Suzunari × Dhaka	" (17)	66	0.95
Suzunari × Dharial	" (21)	70	0.99
Suzunari × Dular	" (18)	67	0.99
Akebono × Dhaka	" (20)	69	0.95
Akebono × Dharial	5 May (24)	78	1.06
Akebono × Dular	30 April (19)	68	0.96
Murasaki Ine	24 April (17)	60	—
Chiyonishiki	30 April (21)	70	—
Suzunari	" (20)	69	—
Akebono	5 May (21)	75	—
Dhaka	30 April (21)	70	—
Dharial	" (23)	72	—
Dular	" (18)	67	—
Average heterosis	—	—	1.00

a : days after transplanting.
Figures in the parentheses indicate days before flowering.
Heterosis = F_1 value / mid-parent value.

Data were analyzed using ANOVA technique. Heterosis was expressed as the ratio between the performance of the F_1 hybrid and the mid-parent value;

$$\text{heterosis} = \frac{F_1 \text{ value}}{\text{mid-parent value}}$$

The mid-parent value was calculated as the average performance of female and male parent;

$$\text{mid-parent value} = \frac{(\text{female parent value} + \text{male parent value})}{2}$$

Results

The flowering time was different among the parent cultivars and F_1 hybrids (Table 1). The difference in the flowering date among the indica cultivars was very small compared to that among the japonica cultivars. Out of 12 F_1 hybrids, 8 flowered earlier than their mid-parent values. Chiyonishiki×Dhaka, Suzunari×Dhaka and Akebono×Dhaka flowered earlier than their parents. The average heterosis for days to flowering was 1.00.

CER was higher at the active tillering stage (17.9-21.4 μmol m^{-2} s^{-1}) than at the flowering (12.3-17.5 μmol m^{-2} s^{-1}) and dough ripe (10.5-15.8 μmol m^{-2} s^{-1}) stages in all parent cultivars and F_1 hybrids (Table 2). At the active tillering stage, 6 F_1 hybrids showed positive heterosis for CER. On average, F_1 hybrids showed a slightly positive heterosis (1.01). At the flowering stage, all the F_1 hybrids except 2, showed positive heterosis for CER, among which Murasaki Ine×Dhaka, Murasaki

Table 2. Leaf CO_2 exchange rate (CER) and heterosis in F_1 hybrids at different stages.

F_1 hybrid / parent	Active tillering stage		Flowering stage		Dough ripe stage	
	CER^{ns} ($\mu mol\ m^{-2}\ s^{-1}$)	Heterosis	CER ($\mu mol\ m^{-2}\ s^{-1}$)	Heterosis	CER ($\mu mol\ m^{-2}\ s^{-1}$)	Heterosis
Murasaki Ine × Dhaka	21.4	1.09	17.2	1.10	15.8	1.05
Murasaki Ine × Dharial	20.0	0.99	—	—	—	—
Murasaki Ine × Dular	20.1	1.07	15.7	1.15	13.9	1.01
Chiyonishiki × Dhaka	19.2	0.99	15.4	1.00	10.5	0.72
Chiyonishiki × Dharial	19.6	0.98	14.1	1.00	12.6	0.93
Chiyonishiki × Dular	18.9	1.02	14.2	1.06	13.9	1.05
Suzunari × Dhaka	19.8	1.01	16.1	1.02	13.6	0.89
Suzunari × Dharial	19.0	0.93	15.4	1.06	14.3	1.00
Suzunari × Dular	19.3	1.02	14.6	1.06	13.4	0.95
Akebono × Dhaka	19.6	0.99	17.5	1.07	15.1	1.02
Akebono × Dharial	20.0	0.98	15.8	1.05	11.4	0.83
Akebono × Dular	20.3	1.07	16.1	1.13	14.4	1.07
Murasaki Ine	19.5	—	14.9	—	15.3	—
Chiyonishiki	19.1	—	14.4	—	14.2	—
Suzunari	19.8	—	15.2	—	15.8	—
Akebono	20.0	—	16.2	—	14.7	—
Dhaka	19.6	—	16.4	—	14.8	—
Dharial	20.9	—	13.9	—	12.9	—
Dular	17.9	—	12.3	—	12.3	—
Average heterosis	—	1.01	—	1.06	—	0.96

ns : F-test was not significant.
Heterosis = F_1 value / mid-parent value.
F-test for all F_1 and parents after active tillering stage was not performed due to uneven flowering time.
Data were not taken when the flowering time of F_1 and its parents differed more than 10 d.

Ine × Dular and Akebono × Dular showed higher heterosis. The average heterosis at this stage was 1.06. At the dough ripe stage, only 5 F_1 hybrids showed heterosis for CER, and a negative average heterosis of 0.96 was found. Murasaki Ine × Dhaka and Akebono × Dular showed a higher CER and high heterosis for CER throughout the growing season.

Out of 12 F_1 hybrids, 9 showed positive heterosis for SPAD value at the active tillering stage (Table 3). The average heterosis for SPAD value was 1.04. At the flowering stage, most F_1 hybrids did not show positive heterosis for SPAD value, but only Chiyonishiki × Dular showed slightly positive heterosis. On average, the heterosis for SPAD value at the flowering stage was negative (0.98). At the dough ripe stage, half of the F_1 hybrids showed positive heterosis for SPAD value, but the average value is only 1.01. No significant correlation ($P=0.136$) was found between heterosis for SPAD value and heterosis for CER at the flowering stage (Fig. 1).

At the active tillering stage, all F_1 hybrids showed positive heterosis for SLA with an average value of 1.09 (Table 4). At the flowering stage, all F_1 hybrids of Murasaki Ine showed negative heterosis for SLA, but the others showed positive heterosis. An average heterosis of 1.03 was observed for SLA. Out of 12 F_1 hybrids, 7 showed positive heterosis at dough ripe stage with an average value of 1.00. A significant negative relation ($P=0.043$) was found between heterosis for SLA and heterosis for CER at the flowering stage (Fig. 2).

Discussion

Heterosis for days to flowering has been reported to be generally negative (Chang et al., 1971; Purohit, 1972; Mallick et al., 1978; Singh et al., 1980; Virmani et al., 1981, 1982). This means that F_1 hybrids flower earlier than their parents. Early flowering is a desirable trait in intensive culture. In the present study, the F_1 hybrids failed to flower early on average, but most of them flowered earlier than their mid-parent values (Table 1). Three of them flowered earlier than either of their parent.

The absolute value of CER was high in all the F_1 hybrids and parent cultivars at the active tillering stage, but most of the F_1 hybrids showed positive heterosis for CER at the flowering stage with positive average value (Table 2). Murayama et al. (1987) also reported positive heterosis for CER and for N content in japonica-japonica hybrids, which were measured 7-10 d after heading. Higher N content in F_1 hybrids might be the possible reason for positive heterosis for CER at the flowering stage in this study, because a number of studies revealed that CER of rice leaf is dependent on leaf N content (Ishihara et al., 1979a, 1979b; Sinclair and Horie, 1989; Tagawa et al., 2000). Two F_1 hybrids

Table 3. Chlorophyll meter reading (SPAD value) and heterosis in F_1 hybrids at different stages.

F_1 hybrid / parent	Active tillering stage		Flowering stage		Dough ripe stage	
	SPAD	Heterosis	SPAD	Heterosis	SPAD	Heterosis
Murasaki Ine × Dhaka	41.0 ab	1.12	36.5	0.94	39.9	0.98
Murasaki Ine × Dharial	38.9 b-e	1.03	—	—	—	—
Murasaki Ine × Dular	40.1 abc	1.10	35.8	0.94	36.8	0.94
Chiyonishiki × Dhaka	38.7 b-e	1.00	35.5	0.98	33.5	0.91
Chiyonishiki × Dharial	40.3 abc	1.02	34.3	0.97	38.3	1.13
Chiyonishiki × Dular	40.9 ab	1.07	36.1	1.01	36.8	1.04
Suzunari × Dhaka	39.5 a-d	1.03	35.7	0.99	37.9	1.01
Suzunari × Dharial	41.6 a	1.06	35.3	1.00	38.3	1.10
Suzunari × Dular	39.5 a-d	1.04	34.3	0.96	36.6	1.01
Akebono × Dhaka	37.6 d-g	0.98	36.4	1.00	34.9	0.98
Akebono × Dharial	39.3 bcd	1.00	35.6	1.00	32.5	0.99
Akebono × Dular	38.8 b-e	1.01	34.7	0.97	35.7	1.04
Murasaki Ine	37.0 efg	—	41.2	—	43.9	—
Chiyonishiki	40.8 ab	—	36.3	—	35.8	—
Suzunari	40.4 abc	—	36.2	—	37.5	—
Akebono	40.7 ab	—	36.7	—	33.8	—
Dhaka	36.4 fg	—	36.1	—	37.6	—
Dharial	38.2 c-f	—	34.2	—	32.1	—
Dular	35.9 g	—	35.0	—	34.8	—
Average heterosis	—	1.04	—	0.98	—	1.01

Heterosis = F_1 value / mid-parent value.
Means followed by the same letter(s) are not significantly different at 5% level by DMRT.
F-test and mean comparison among all F_1 and parents after active tillering stage were not performed due to uneven flowering time.
Data were not taken when the flowering time of F_1 and its parents differed more than 10 d.

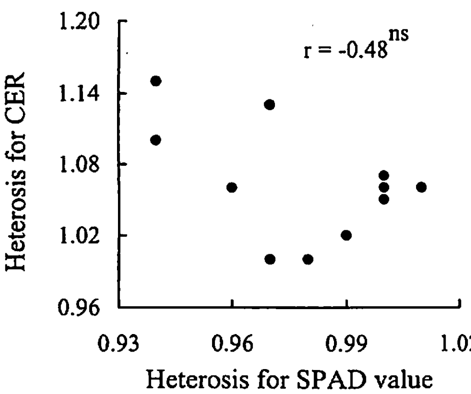

Fig. 1. Relationship between heterosis for SPAD value and heterosis for CER at flowering stage. ns : not significant.

showed higher positive heterosis throughout the growing season in the present study. It has been reported that CER of a rice leaf reaches its maximum about 10 d after full expansion, and then declines steadily (Makino et al., 1983, 1984a). In the present study, the fully expanded and most recently matured flag leaf blade was used for CER measurement at the flowering stage and the same leaf blade was used for measurement at the dough ripe stage. Therefore, the lower CER observed at the dough ripe stage in the present study might be attributed to the leaf aging with decreasing leaf N content (Makino et al., 1984b). At the dough ripe stage, average heterosis for CER was negative (Table 2). Makino et al. (1984b) also stated that leaf N content was not always associated with RuBP carboxylase content in senescing leaf and thus N content of senescing leaf did not necessarily indicate photosynthetic activity. Therefore, some F_1 hybrids might have failed to show positive heterosis due to low photosynthetic activity at the dough ripe stage.

SLA in most F_1 hybrids and parent cultivars decreased from the active tillering stage up to the dough ripe stage (Table 4). This means that leaves became thicker at later stages. At the active tillering stage heterosis for SLA was 1.09 suggesting that leaves of F_1 hybrids were thinner than their parents at early stage. But the photosynthetic rate in the F_1 hybrids was at par with their parent cultivars at this stage (Table 2). Subsequently, leaves of F_1 hybrids became thicker which can be understood by decreasing heterosis for SLA (Table 4).

The relationship between heterosis for SPAD value and that for CER, and between heterosis for SLA and that for CER were examined at the flowering stage, because average heterosis value for CER was positive and high at this stage. In this study, chlorophyll content (SPAD value) was not correlated with CER. Saka (1985) reported that photosynthetic rate showed a lower correlation with chlorophyll content than with other photosynthetic parameters such as Rubisco activity and

Table 4. Specific leaf area (SLA) and heterosis in F_1 hybrids at different stages.

F_1 hybrid / parent	Active tillering stage		Flowering stage		Dough ripe stage	
	SLA ($cm^2 g^{-1}$)	Heterosis	SLA ($cm^2 g^{-1}$)	Heterosis	SLA ($cm^2 g^{-1}$)	Heterosis
Murasaki Ine × Dhaka	285.3 ab	1.07	260.1 b	0.97	257.1 b	1.07
Murasaki Ine × Dharial	290.0 a	1.11	218.3 j	0.84	216.1 hi	0.87
Murasaki Ine × Dular	283.2 ab	1.08	257.0 bc	0.96	273.7 a	1.09
Chiyonishiki × Dhaka	254.8 gh	1.06	240.4 f	1.03	229.1 ef	1.03
Chiyonishiki × Dharial	258.4 efg	1.11	238.0 fg	1.06	191.2 k	0.83
Chiyonishiki × Dular	272.4 cd	1.16	239.8 f	1.02	246.4 c	1.05
Suzunari × Dhaka	245.1 hi	1.02	251.6 cd	1.11	227.1 efg	1.03
Suzunari × Dharial	250.7 ghi	1.08	227.3 hi	1.04	204.7 j	0.89
Suzunari× Dular	266.3 def	1.14	237.3 fg	1.05	231.0 ef	0.99
Akebono × Dhaka	255.9 fgh	1.01	248.6 de	1.06	244.7 cd	1.15
Akebono × Dharial	285.8 ab	1.15	259.1 bc	1.14	204.8 j	0.92
Akebono × Dular	268.2 cde	1.08	241.7 ef	1.02	230.1 ef	1.02
Murasaki Ine	278.6 bc	—	294.6 a	—	260.9 b	—
Chiyonishiki	224.0 j	—	228.1 hi	—	227.7 efg	—
Suzunari	223.9 j	—	216.1 j	—	223.2 fgh	—
Akebono	252.6 ghi	—	230.9 gh	—	208.0 ij	—
Dhaka	256.5 fgh	—	239.2 f	—	218.7 gh	—
Dharial	242.4 i	—	222.1 ij	—	235.1 de	—
Dular	245.1 hi	—	243.0 ef	—	241.7 cd	—
Average heterosis	—	1.09	—	1.03	—	1.00

Heterosis = F_1 value / mid-parent value.
Means within a column followed by the same letter(s) are not significantly different at 5% level by DMRT.

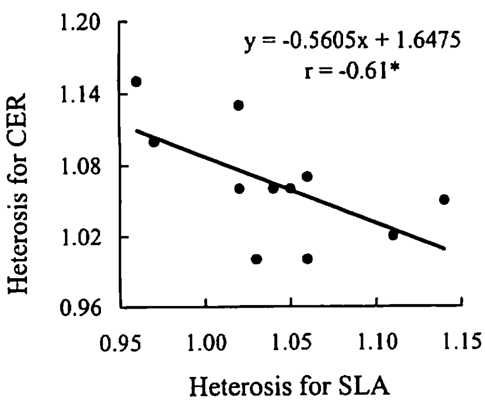

Fig. 2. Relationship between heterosis for SLA and heterosis for CER at flowering stage. * : significant at 5% level.

soluble protein content throughout the growing period. A negative relation between CER and SLA at the flowering stage suggested that CER was dependent on thickness of leaf. However, heterosis for both CER and SLA were positive at this stage suggesting that the heterosis for CER was dependent not only on negative heterosis for SLA but also on other photosynthetic factors such as N content, soluble protein content and Rubisco activity.

Although an extra small dose of N fertilizer was applied at the active tillering stage, some F_1 hybrids failed to show positive heterosis for CER, but an average positive heterosis was observed at the flowering stage. However, further studies with different levels of N at different growth stages may be needed to evaluate the photosynthetic potential of the F_1 hybrids of rice. Determination of N content, soluble protein content and Rubisco activity, which are biochemical factors related to photosynthesis, may elucidate the cause of heterosis for CER.

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