Plant Prod. Sci. 4(3) : 202—209 (2001)

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

II. Heterosis for leaf area and dry matter accumulation

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Abstract: A pot experiment was conducted to investigate the heterosis for morphological characters and to examine the relationship among some characters at active tillering, flowering and dough ripe stages of 12 F_1 hybrids from crosses between japonica and indica rice. Heterosis for plant height, number of tillers, green leaf area and dry matter accumulation per plant was positive at all stages. The intensity of heterosis was higher at the active tillering stage for number of tillers, leaf area and dry matter accumulation per plant. A significant positive relationship was found between tiller number and leaf area per plant at active tillering and flowering stages. Significant positive relationships between leaf area and dry matter accumulation, and between tiller number and dry matter accumulation per plant were observed at all stages. A significant positive relationship was found between leaf area per plant at an early stage and dry matter accumulation per plant at a later stage, suggesting that early development of leaf area is an important factor for higher dry matter accumulation in F_1 hybrids. Although heterosis for percent dead leaf blade was positive at the flowering stage due to early leaf senescence in some F_1 hybrids, a larger leaf area was also found in F_1 hybrids at this stage and leaves of F_1 hybrids remained green longer compared to parent cultivars up to the dough ripe stage.

Key words: Dry matter, F_1 hybrid, Heterosis, Leaf area.

The economic significance of heterosis in crop breeding has been widely appreciated since the successful introduction of hybrid maize varieties. The phenomenon of heterosis has been clearly demonstrated in rice, manifested in several agronomic, physiological and biochemical traits.

Research on commercial exploitation of heterosis in rice has been carried out in different countries (Richaria, 1962; Stansel and Craigmiles, 1966; Virmani, 1994). Murayama et al. (1974) discussed the advantages of utilizing hybrid vigour under field conditions. F_1 hybrids have been reported to have a higher tillering ability, larger leaf area and greater dry matter accumulation at the vegetative growth stages (Kawano et al., 1969; Govinda Raj and Siddiq, 1986; Khan et al., 1998a). However, most of the studies in the past were made with indica-indica crosses or a few japonica-japonica crosses. In contrast to the numerous studies on agronomic traits of intra-subspecific heterosis, very few studies on morphological traits of inter-subspecific heterosis have been carried out. Literature regarding heterosis for different morphological traits at different growth stages of the same cross of rice is also very limited. Studies on heterosis for morphology at different growth stages should be carried out thoroughly, because the yield potential of rice is influenced by stem reserves before flowering, dry matter production during the grain filling period and green leaf area duration (Kropff et al., 1994).

In this study, heterosis for different morphological traits was determined at different growth stages of F_1 hybrids from crosses between japonica and indica rice. The relationship among traits at the same growth stages, and also between leaf area at an early stage and dry matter at a later stage was examined to elucidate the morphological characters responsible for higher dry matter accumulation in 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 singly into 0.02 m^2 Wagner pots containing Shimajiri Mahji (dark reddish)

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Abbreviations: BP, better parent; DAT, days after transplanting; F_1, first filial generation; MP, mid-parent.

soil distributed in the Okinawa region. Organic matter "Minori" was added at the rate of 3 kg m^{-2} and a basal 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 and second top dressings of N were applied at the rate of 2.9 g m^{-2} at 14 and 28 d after transplanting (DAT), respectively. 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. 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.

Data on plant height, and number of tillers, green leaf area and dry matter accumulation per plant were taken 3 times during the growing period *viz.*, at active tillering, flowering (when 50% plants flowered) and dough ripe (12-13 d after flowering) stages. Percent dead leaf blade was measured at flowering and dough ripe stages. Five plants from each F_1 hybrid or parent cultivar were sampled at each sampling time. Plant height was from the base of the hill to the tip of the highest leaf or panicle, which was highest. Aboveground parts of plants were harvested, from which leaf blades were separated. Dead leaf blades and dead portion of leaf blades were also separated carefully from the green portion. The area of the green leaf blades and green portion of leaf blades was measured immediately with an automatic area meter (AAM-8, Hayashi Denkoh Co. Ltd., Japan). The dry matter of each component was measured after oven drying at 80°C to a constant weight. The percent dead leaf blade was expressed on a dry weight basis and calculated according to the following formula,

$$\%\ \text{dead leaf blade} = \frac{\text{Weight of dead leaf blade} + \text{dead portion of leaf blade}}{\text{Total weight of leaf blade}} \times 100$$

Data were analyzed using ANOVA technique. *F*-test and mean comparison of percent dead leaf blade were performed with transformed data by square root {$\sqrt{x}$ for data sets containing less than 30%} or arc sine {arc sin $\sqrt{(\text{percentage})}$ for data sets containing 0-70%} transformation technique (Gomez and Gomez, 1984).

Heterosis over the mid-parent value was expressed as the ratio between the performance of the F_1 hybrid and the mid-parent value ;

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

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

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

Heterosis over better parent was expressed as the ratio between the performance of the F_1 hybrid and the better parent;

$$\text{heterosis (over better parent)} = \frac{F_1 \text{ value}}{\text{better parent value}}$$

Results

The plant height of japonica cultivars were shorter than the indica cultivars at flowering and dough ripe stages except Murasaki Ine, which resembled indica cultivar Dular (Table 1). All F_1 hybrids showed positive heterosis over the mid-parent at active tillering and dough ripe stages except Chiyonishiki×Dharial. At the flowering stage, out of 12 F_1 hybrids, 7 showed heterosis over the mid-parent. Most F_1 hybrids showed heterosis over the better parent at the active tillering stage. Some of them showed heterosis over the better parent also at flowering and dough ripe stages. On the average, the heterosis over mid-parent was 1.09, 1.04 and 1.09 at active tillering, flowering and dough ripe stages, respectively. At the active tillering stage, on the average a heterosis of 1.05 over the better parent was also found.

The number of tillers per plant increased up to the flowering stage and then decreased at the dough ripe stage in most of F_1 hybrids and parent cultivars (Table 2). Most F_1 hybrids showed positive heterosis over both the mid-parent and better parent for tiller number at all stages. The average heterosis over the mid-parent at the active tillering stage was highly positive with a value of 1.22, which decreased at the flowering stage (1.13) and was maintained similarly up to the dough ripe stage (1.14). At active tillering and flowering stages, average positive heterosis over better parent was also found.

All F_1 hybrids and parent cultivars had a greater leaf area up to the flowering stage, which decreased at the dough ripe stage, but was still higher than the active tillering stage, except parent cultivar Dhaka (Table 3). All the F_1 hybrids showed positive heterosis over both mid-parent and better parent for leaf area at active tillering and dough ripe stages. At flowering stage, out of 12 F_1 hybrids, 8 showed positive heterosis over mid-parent and 7 showed over better parent. On an average, positive heterosis over both the mid-parent and better parent was maintained throughout the growing season. A higher positive heterosis over the mid-parent was found at the active tillering stage (1.39) and dough ripe stage (1.33). A significant positive correlation was found between number of tillers and leaf area per plant at active tillering ($P = 0.001$) and flowering ($P = 0.007$) stages (Fig. 1A and 1B).

No dead leaf blades or dead portions of leaf blades were found at the active tillering stage. The percent dead leaf blade was higher in all indica cultivars and Akebono than in other japonica cultivars at both flowering and dough ripe stages (Table 4). At the flowering stage, the percent dead leaf blade was higher in some F_1 hybrids. Out of 12 F_1 hybrids, 5 showed positive heterosis over the mid-parent for the dead leaf blade at the flowering stage. Out of them only 3 showed positive heterosis over the better parent. At the dough ripe stage, only 2 showed

Table 1. Plant height and heterosis in F_1 hybrids at different stages.

F_1 hybrid / parent	Active tillering stage			Flowering stage			Dough ripe stage		
	Plant height (cm)	Heterosis		Plant height (cm)	Heterosis		Plant height (cm)	Heterosis	
		Over MP	Over BP		Over MP	Over BP		Over MP	Over BP
Murasaki Ine × Dhaka	92.6 a	1.14	1.13	114.6 a	1.10	1.01	118.0 bc	1.07	1.03
Murasaki Ine × Dharial	84.7 c-f	1.11	1.03	97.2 bcd	0.91	0.85	122.3 ab	1.12	1.07
Murasaki Ine × Dular	88.0 bc	1.09	1.07	112.1 a	1.00	0.99	125.4 a	1.09	1.08
Chiyonishiki × Dhaka	79.9 ghi	1.02	0.99	98.8 bcd	1.09	1.04	103.1 g	1.07	0.97
Chiyonishiki × Dharial	72.1 lm	0.99	0.96	89.5 ef	0.96	0.90	95.8 h	1.00	0.91
Chiyonishiki × Dular	83.5 d-g	1.08	1.06	100.4 bc	1.02	0.90	112.6 cde	1.11	0.97
Suzunari × Dhaka	89.0 ab	1.13	1.10	103.2 b	1.11	1.09	105.2 fg	1.06	0.99
Suzunari × Dharial	80.7 f-i	1.10	1.05	92.0 def	0.96	0.92	102.4 g	1.04	0.98
Suzunari × Dular	86.3 bcd	1.11	1.09	112.6 a	1.11	1.01	113.6 cd	1.09	0.98
Akebono × Dhaka	81.8 e-h	1.08	1.01	97.6 bcd	1.10	1.03	109.5 d-g	1.15	1.03
Akebono × Dharial	74.2 kl	1.06	1.06	91.2 def	1.00	0.91	111.1 c-f	1.18	1.06
Akebono × Dular	85.3 b-e	1.14	1.08	102.4 bc	1.06	0.92	105.9 efg	1.06	0.91
Murasaki Ine	82.0 e-h	—	—	113.7 a	—	—	114.3 cd	—	—
Chiyonishiki	75.2 jkl	—	—	86.1 fg	—	—	87.6 ij	—	—
Suzunari	76.9 ijk	—	—	91.4 def	—	—	92.1 hi	—	—
Akebono	70.1 m	—	—	82.4 g	—	—	84.0 j	—	—
Dhaka	80.9 f-i	—	—	95.0 cde	—	—	106.0 efg	—	—
Dharial	70.1 m	—	—	100.0 bc	—	—	104.8 fg	—	—
Dular	79.0 hij	—	—	111.4 a	—	—	116.1 bcd	—	—
Average heterosis	—	1.09	1.05	—	1.04	0.96	—	1.09	1.00

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

Table 2. Number of tillers per plant and heterosis in F_1 hybrids at different stages.

F_1 hybrid / parent	Active tillering stage			Flowering stage			Dough ripe stage		
	Number of tillers plant^{-1}	Heterosis		Number of tillers plant^{-1}	Heterosis		Number of tillers plant^{-1}	Heterosis	
		Over MP	Over BP		Over MP	Over BP		Over MP	Over BP
Murasaki Ine × Dhaka	9.4 b-e	1.13	0.89	10.2 b-e	1.21	1.13	9.6 bcd	1.32	1.12
Murasaki Ine × Dharial	8.8 d-g	1.40	1.33	10.0 b-e	1.22	1.16	7.8 def	1.18	1.08
Murasaki Ine × Dular	6.8 h-k	1.19	1.13	6.8 hi	0.97	0.87	5.6 gh	1.04	0.93
Chiyonishiki × Dhaka	11.8 a	1.31	1.11	11.8 ab	1.27	1.23	10.8 bc	1.24	1.23
Chiyonishiki × Dharial	9.0 c-f	1.29	1.22	10.8 a-d	1.19	1.13	9.6 bcd	1.20	1.09
Chiyonishiki × Dular	7.6 f-i	1.19	1.03	7.4 ghi	0.94	0.77	6.8 fg	1.00	0.77
Suzunari × Dhaka	10.2 bcd	1.09	0.96	10.2 b-e	1.15	1.13	9.2 cd	1.08	1.07
Suzunari × Dharial	9.0 c-f	1.22	1.10	9.8 b-f	1.13	1.11	8.8 de	1.13	1.05
Suzunari × Dular	8.8 d-g	1.29	1.07	7.8 f-i	1.04	0.89	6.8 fg	1.03	0.81
Akebono × Dhaka	11.8 a	1.11	1.11	12.4 a	1.20	1.07	12.8 a	1.31	1.16
Akebono × Dharial	10.4 abc	1.21	0.98	11.6 abc	1.15	1.00	9.4 bcd	1.03	0.85
Akebono × Dular	9.4 b-e	1.18	0.89	9.6 c-f	1.08	0.83	8.8 de	1.11	0.80
Murasaki Ine	6.0 jk	—	—	7.8 f-i	—	—	6.0 gh	—	—
Chiyonishiki	7.4 g-j	—	—	9.6 c-f	—	—	8.8 de	—	—
Suzunari	8.2 e-h	—	—	8.8 d-g	—	—	8.4 def	—	—
Akebono	10.6 ab	—	—	11.6 abc	—	—	11.0 b	—	—
Dhaka	10.6 ab	—	—	9.0 d-g	—	—	8.6 de	—	—
Dharial	6.6 ijk	—	—	8.6 e-h	—	—	7.2 efg	—	—
Dular	5.4 k	—	—	6.2 i	—	—	4.8 h	—	—
Average heterosis	—	1.22	1.07	—	1.13	1.03	—	1.14	1.00

For footnote, see Table 1.

Table 3. Leaf area per plant and heterosis in F_1 hybrids at different stages.

F_1 hybrid / parent	Active tillering stage			Flowering stage			Dough ripe stage		
	Leaf area	Heterosis		Leaf area	Heterosis		Leaf area	Heterosis	
	(cm^2)	Over MP	Over BP	(cm^2)	Over MP	Over BP	(cm^2)	Over MP	Over BP
Murasaki Ine × Dhaka	674.7 bc	1.43	1.07	952.0 bc	1.24	1.22	851.6 ab	1.64	1.60
Murasaki Ine × Dharial	585.0 de	1.46	1.19	901.2 b-e	1.14	1.09	777.7 bcd	1.39	1.33
Murasaki Ine × Dular	518.6 ef	1.33	1.09	757.5 f	0.98	0.96	684.2 def	1.33	1.28
Chiyonishiki × Dhaka	702.1 ab	1.43	1.11	973.2 b	1.24	1.22	717.2 cde	1.30	1.21
Chiyonishiki × Dharial	524.8 ef	1.25	1.07	799.5 def	0.99	0.97	671.0 def	1.14	1.13
Chiyonishiki × Dular	521.3 ef	1.26	1.10	761.4 f	0.96	0.96	721.9 cde	1.32	1.21
Suzunari × Dhaka	657.2 bcd	1.32	1.04	962.8 b	1.26	1.23	671.1 def	1.22	1.14
Suzunari × Dharial	584.1 de	1.37	1.19	767.3 ef	0.98	0.93	664.5 def	1.13	1.13
Suzunari × Dular	602.7 cd	1.44	1.27	930.7 bcd	1.21	1.17	737.6 cde	1.36	1.25
Akebono × Dhaka	758.6 a	1.47	1.20	902.4 b-e	1.10	1.05	807.6 bc	1.41	1.27
Akebono × Dharial	633.2 bcd	1.42	1.29	1144.1 a	1.36	1.33	943.9 a	1.55	1.49
Akebono × Dular	632.4 bcd	1.45	1.33	843.2 b-f	1.02	0.98	639.5 efg	1.13	1.01
Murasaki Ine	308.2 h	—	—	751.8 f	—	—	533.1 gh	—	—
Chiyonishiki	351.3 gh	—	—	795.0 ef	—	—	594.8 fgh	—	—
Suzunari	360.6 gh	—	—	743.6 f	—	—	589.2 fgh	—	—
Akebono	400.9 g	—	—	859.4 b-f	—	—	635.1 efg	—	—
Dhaka	633.2 bcd	—	—	780.4 ef	—	—	506.5 h	—	—
Dharial	490.6 f	—	—	827.3 c-f	—	—	583.6 fgh	—	—
Dular	474.1 f	—	—	792.7 ef	—	—	496.8 h	—	—
Average heterosis	—	1.39	1.16	—	1.12	1.09	—	1.33	1.25

For footnote, see Table 1.

Table 5. Dry matter accumulation per plant and heterosis in F_1 hybrids at different stages.

F_1 hybrid / parent	Active tillering stage			Flowering stage			Dough ripe stage		
	Dry matter	Heterosis		Dry matter	Heterosis		Dry matter	Heterosis	
	(g)	Over MP	Over BP	(g)	Over MP	Over BP	(g)	Over MP	Over BP
Murasaki Ine × Dhaka	4.5 c	1.30	0.96	15.5 hi	1.14	0.84	22.4 bc	1.29	1.01
Murasaki Ine × Dharial	3.7 de	1.23	0.97	20.5 abc	1.52	1.13	24.0 b	1.45	1.16
Murasaki Ine × Dular	3.6 def	1.22	0.97	12.2 j	0.98	0.76	18.3 de	1.18	0.99
Chiyonishiki × Dhaka	5.7 ab	1.48	1.21	19.6 b-e	1.15	1.07	23.5 b	1.20	1.06
Chiyonishiki × Dharial	3.8 d	1.12	1.00	17.8 c-h	1.05	0.98	23.7 b	1.25	1.15
Chiyonishiki × Dular	3.6 def	1.07	0.97	17.2 e-i	1.08	1.07	19.1 cde	1.07	1.03
Suzunari × Dhaka	5.6 b	1.44	1.19	20.0 bcd	1.20	1.09	23.5 b	1.19	1.06
Suzunari × Dharial	4.5 c	1.30	1.18	18.7 b-f	1.13	1.03	23.1 b	1.21	1.12
Suzunari × Dular	4.6 c	1.35	1.24	19.7 b-e	1.27	1.22	22.3 bc	1.24	1.21
Akebono × Dhaka	6.2 a	1.61	1.32	21.2 ab	1.13	1.12	28.2 a	1.26	1.25
Akebono × Dharial	4.6 c	1.35	1.21	22.8 a	1.23	1.20	27.9 a	1.29	1.24
Akebono × Dular	5.1 bc	1.52	1.38	17.5 d-i	1.00	0.92	21.3 bcd	1.04	0.94
Murasaki Ine	2.2 h	—	—	8.8 k	—	—	12.6 f	—	—
Chiyonishiki	3.0 fg	—	—	15.7 ghi	—	—	17.2 e	—	—
Suzunari	3.1 efg	—	—	15.0 i	—	—	17.5 e	—	—
Akebono	3.0 fg	—	—	19.0 b-e	—	—	22.6 bc	—	—
Dhaka	4.7 c	—	—	18.4 c-g	—	—	22.1 bc	—	—
Dharial	3.8 d	—	—	18.2 c-h	—	—	20.6 b-e	—	—
Dular	3.7 de	—	—	16.1 f-i	—	—	18.4 de	—	—
Average heterosis	—	1.33	1.13	—	1.16	1.04	—	1.22	1.10

For footnote, see Table 1.

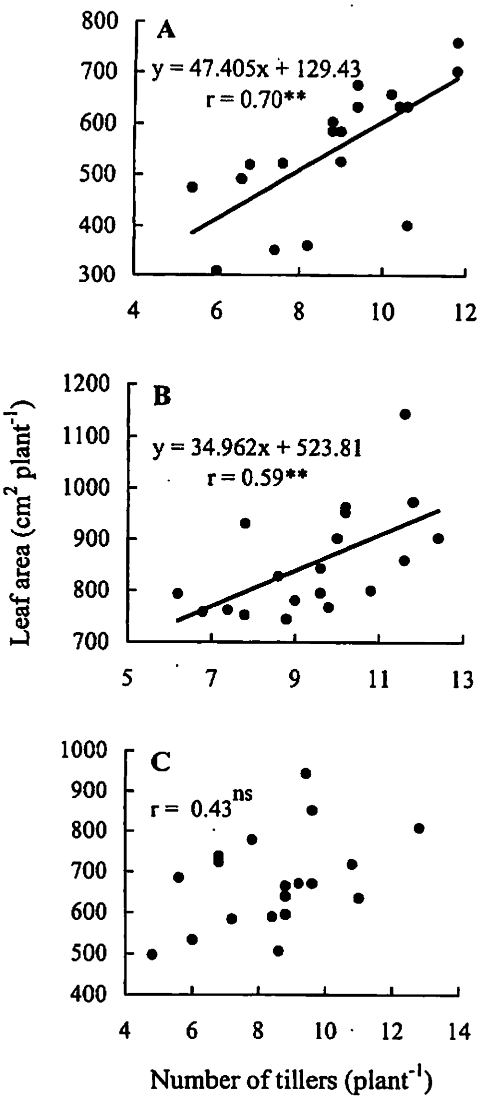

Fig. 1. Relationship between number of tillers and leaf area per plant at active tillering (A), flowering (B) and dough ripe (C) stages. ** and ns : significant at 1% level and not significant, respectively.

positive heterosis over the mid-parent. Non of the F_1 hybrids showed positive heterosis over the better parent at this stage. On average, a positive heterosis of 1.22 over the mid-parent was found only at the flowering stage.

All F_1 hybrids showed positive heterosis over the mid-parent for dry matter accumulation at active tillering and dough ripe stages (Table 5). At the flowering stage, out of 12 F_1 hybrids 10 showed positive heterosis over the mid-parent. Most F_1 hybrids showed positive heterosis over the better parent throughout the growing season. On average, positive heterosis over both mid-parent and better parent was also observed throughout the growing season. The magnitude of heterosis over both mid-parent and better parent was higher at the active tillering stage (1.33, 1.13), became lower at the flowering stage (1.16, 1.04) and increased at the dough ripe stage (1.22, 1.10). There was a significant positive

Table 4. Percent dead leaf blade (dry weight basis) and heterosis in F_1 hybrids at different stages.

F_1 hybrid / parent	Flowering stage			Dough ripe stage		
	% dead leaf blade	Heterosis Over MP	Heterosis Over BP	% dead leaf blade	Heterosis Over MP	Heterosis Over BP
Mura × Dhaka	9.4 ij	1.20	0.63	20.0 efg	0.73	0.49
Mura × Dharial	23.9 a	2.78	1.45	28.8 bcd	1.24	0.89
Mura × Dular	6.7 kl	0.99	0.52	18.6 fgh	0.76	0.53
Chiyo × Dhaka	8.5 jk	0.79	0.57	20.5 efg	0.66	0.50
Chiyo × Dharial	19.5 b	1.69	1.18	24.5 def	0.92	0.76
Chiyo × Dular	12.1 fgh	1.25	0.95	12.5 i	0.45	0.36
Suzu × Dhaka	11.1 ghi	0.96	0.74	21.1 efg	0.73	0.51
Suzu × Dharial	19.8 b	1.61	1.20	26.3 cde	1.06	0.81
Suzu × Dular	8.6 jk	0.82	0.67	14.5 hi	0.56	0.41
Ake × Dhaka	14.1 def	0.87	0.81	31.3 bc	0.88	0.76
Ake × Dharial	16.9 bcd	1.00	0.97	24.4 def	0.78	0.75
Ake × Dular	9.9 hij	0.66	0.57	24.4 def	0.74	0.70
Murasaki Ine	0.7 m	—	—	13.9 hi	—	—
Chiyonishiki	6.6 l	—	—	20.8 efg	—	—
Suzunari	8.1 jkl	—	—	17.1 ghi	—	—
Akebono	17.4 bc	—	—	30.5 bcd	—	—
Dhaka	15.0 cde	—	—	41.0 a	—	—
Dharial	16.5 cd	—	—	32.4 bc	—	—
Dular	12.8 efg	—	—	35.1 ab	—	—
Average heterosis	—	1.22	0.86	—	0.79	0.62

Mura, Murasaki Ine ; Chiyo, Chiyonishiki ; Suzu, Suzunari ; Ake, Akebono.
MP, mid-parent ; BP, better parent.
Heterosis (over MP) = F_1 value /MP value, Heterosis (over BP) = F_1 value /BP value.
Means within a column followed by the same letter (s) are not significantly different at 5% level by DMRT.

correlation between leaf area and dry matter accumulation per plant at active tillering ($P<0.001$), flowering ($P=0.002$) and dough ripe ($P=0.001$) stages (Fig. 2). A similar relationship was also found between tiller number and dry matter accumulation per plant at active tillering ($P<0.001$), flowering ($P=0.004$) and dough ripe ($P=0.001$) stages (Fig. 3). There was a significant positive correlation between leaf area at the active tillering stage and dry matter accumulation at the flowering stage ($P=0.002$), and also between leaf area at the flowering stage and dry matter accumulation at the dough ripe stage ($P=0.001$) (Fig. 4).

Discussion

Virmani (1994) reported that positive heterosis for plant height in rice is common, although there were a few cases of negative heterosis (Singh and Singh, 1978). In this study, most of the F_1 hybrids showed positive heterosis over the mid-parent throughout the growing season (Table 1). Since plant height is negatively correlated with lodging resistance (Chang, 1967), positive heterosis for plant height is not considered desirable. In this study, some of the F_1 hybrids were shorter than one of their

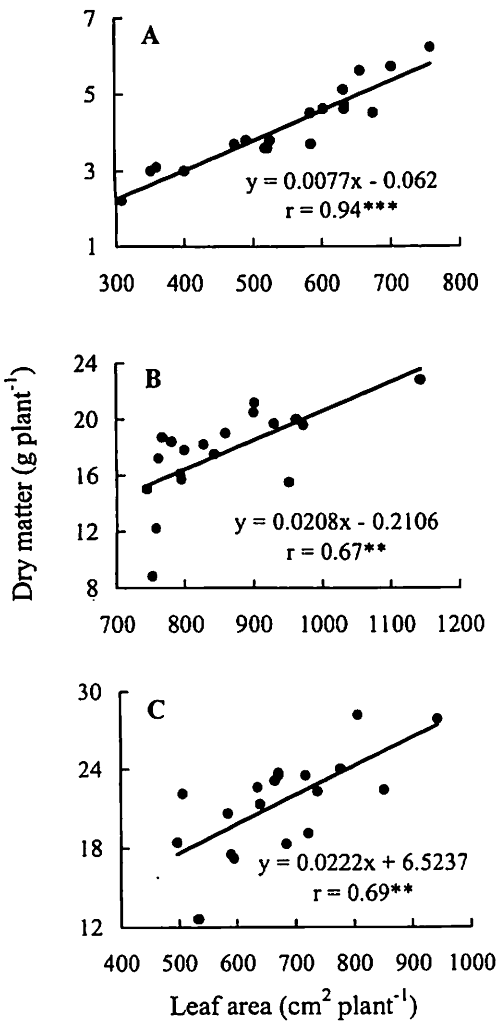

Fig. 2. Relationship between leaf area and dry matter per plant at active tillering (A), flowering (B) and dough ripe (C) stages. *** and ** : significant at 0.1 and 1% level, respectively.

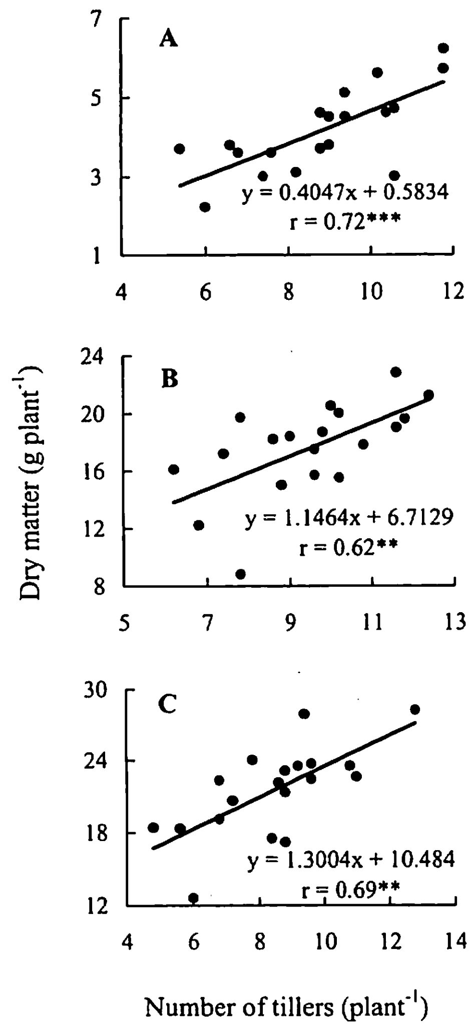

Fig. 3. Relationship between number of tillers and dry matter per plant at active tillering (A), flowering (B) and dough ripe (C) stages. *** and ** : significant at 0.1 and 1% level, respectively.

parents at flowering and dough ripe stages.

The average heterosis for the number of tillers per plant was higher throughout the growing season (Table 2). The magnitude of heterosis for tiller number was higher at the active tillering stage than later stages suggesting that F_1 hybrids were able to produce tillers earlier at a higher rate.

F_1 hybrids showed higher positive heterosis for leaf area at the active tillering stage (Table 3). This means that F_1 hybrids can increase leaf area rapidly than their parent cultivars at early stage. At the flowering stage, the value of heterosis for leaf area was comparatively low. This might be due to increasing leaf area of parent cultivars and/or early leaf senescence of F_1 hybrids (Table 4). The value of heterosis for leaf area increased again at the dough ripe stage. This might be attributed by the rapid senescence of the leaf in some parent cultivars, particularly in the indica types (Table 4). However, most of the F_1 hybrids showed positive heterosis for leaf area throughout the growing season. Larger leaf area in F_1 plants was also reported in other studies (Kawano et al., 1969). In rice, leaf and tiller emerge from the same node (Yoshida, 1981). Thus, the higher number of tillers in the F_1 hybrids led to a more active leaf aerial development in the early growth stage (Fig. 1). However, at the dough ripe stage, the relationship between tiller number and leaf area was not significant (Fig. 1C). This might be due to the rapid leaf senescence of some parent cultivars.

The average heterosis for percent dead leaf blade over mid-parent value was positive at flowering stage due to larger leaf senescence of some F_1 hybrids (Table 4). Sarker et al. (2001) found that some F_1 hybrids of the same cross combinations showed negative heterosis for SPAD value i.e., contained low N compared to their parents at this stage. Moreover, F_1 hybrids were able to produce a larger leaf area compared to parent cultivars. Therefore, leaf senescence started earlier in some F_1

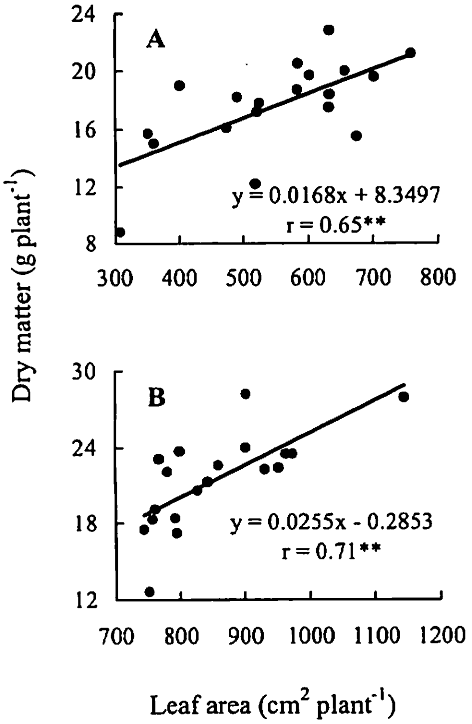

Fig. 4. Relationship between leaf area (LA) per plant at early stage and dry matter (DM) per plant at later stage. (A, between LA at active tillering and DM at flowering stage ; B, between LA at flowering and DM at dough ripe stage.) ** : significant at 1% level.

hybrids due to shortage of N content and mutual shading (Tanaka et al., 1966). Negative heterosis for dead leaf blades at the dough ripe stage might be due to the rapid leaf senescence of some parent cultivars after flowering. Although leaf senescence started early in some F_1 hybrids, the senescence rate was higher in most of the parent cultivars after flowering. This means that the leaves of the F_1 hybrids remained green longer than their parent cultivars during the grain filling period.

Heterosis for dry matter accumulation was always positive and high (Table 5). The magnitude was higher at the early growth stage and also at the dough ripe stage. This might be due to the higher crop growth rate at both stages (Kabaki, 1993). It was found that dry matter accumulation depended on leaf area and number of tillers at all stages (Fig. 2 and 3). Some F_1 hybrids of the same cross combinations showed positive heterosis for photosynthetic rate in terms of CO_2 exchange rate at the active tillering stage (Sarker et al., 2001). Most F_1 hybrids showed positive heterosis also at the flowering stage. Development of larger leaf area with higher CER might result in a greater rate of photosynthesis per plant in F_1 hybrids. As a result, a higher positive heterosis for dry matter accumulation was observed in F_1 hybrids throughout the growing period. The relationship between leaf area at early stages and dry matter accumulation at later stages suggested that early development of larger leaf area contributed to dry matter accumulation at later stage (Fig. 4).

F_1 hybrids were able to produce a larger number of tillers rapidly, which led to early development of leaf area. A large leaf area contributed to higher dry matter production in F_1 hybrids. Although a rapid decline of leaf area in japonica-japonica hybrids was reported (Khan et al., 1998b), a higher positive heterosis for leaf area was found even at the dough ripe stage in this study. Higher dry matter accumulation indicates higher stem reserve. Since the stem reserve and green leaf area were higher, especially at the dough ripe stage, we can expect a higher grain yield from these F_1 hybrids of japonica-indica crosses if inter-subspecific hybrid sterility does not occur. Therefore, experiments should be done to determine the heterosis for yield and yield attributes.

Acknowledgement

We are much indebted to Prof. T. Kobata of Shimane University for supplying the seeds of indica cultivars.

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