Physiology

Physio-morphological Studies of F_1 Hybrids in Rice (*Oryza sativa* L.)

Photosynthetic ability and yield

Md. Nurul Alam Khan, Seiichi Murayama*, Yukio Ishimine*, Eiji Tsuzuki** and Ichiro Nakamura*

(*United Graduate School of Agricultural Sciences, Kagoshima University, Kagoshima 890-0065, Japan ;*
*Faculty of Agriculture, University of the Ryukyus, Nishihara, Okinawa 903-0129, Japan ;
**Faculty of Agriculture, Miyazaki University, Miyazaki 889-2192, Japan)
Accepted 15 June 1998

Abstract : Photosynthetic ability in terms of CO_2 exchange rate and leaf area, dry matter accumulation (dry weight) and other important growth components along with yield and yield contributing characters in two F_1 hybrids of Akebono $\times$ Chiyonishiki (A $\times$ C) and Zenith $\times$ Akebono (Z $\times$ A) were studied. The photosynthetic rate at the flowering stage was lower than that at the panicle initiation stage in all the inbred parent cultivars and F_1 hybrids. Heterosis in photosynthetic rate was higher at the panicle initiation stage than that at the flowering stage. Pre-anthesis leaf area in the F_1 hybrid was significantly larger than that in the parent cultivars. However, the post- anthesis decline in leaf area was more rapid in the F_1 hybrids than in the parent cultivars and its magnitude was the highest in the F_1 hybrid of Z $\times$ A which was tall having long and curved panicles. Pre-anthesis dry matter accumulation in both hybrids was significantly higher in the F_1 plants than the parental cultivars, but post-anthesis dry matter accumulation in the F_1 hybrid was lower than the mid-parental value in Z $\times$ A. The degree of heterosis in grain yield varied with the hybrid combination, an average heterosis being 1.03. Heterosis in grain yield was closely associated with heterosis in harvest index.

Key words : CO_2 exchange rate, Dry matter, F_1 hybrid, Heterosis, Leaf area, Yield.

Commercial exploitation of heterosis in grain yield in rice was established after its successful introduction in China during the 1970s. F_1 hybrids in rice produced 20 $\sim$30% higher yield over the best available inbred parent cultivars in replicated yield trials in China (Lin and Yuan, 1980). This aroused genuine interest among plant breeders and agronomists regarding F_1 hybrids in rice. A large number of studies dealt with the heterosis in grain yield, but only a·few of them discussed the morpho-physiological causes of heterosis in grain yield. The 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 (Govinda Raj and Siddiq, 1986 ; Khan et al., 1997). On the contrary, high vegetative growth did not always result in high yield in the F_1 hybrids. In a few earlier studies e.g., Jennings (1967), Kawano et al. (1969) observed heterosis in vegetative growth, however, failed to find any heterosis for grain yield in the same crosses. F_1 hybrids are commonly taller than the mean heights of parents (Virmani, 1994) and taller plant canopy are usually inefficient in radiation interception. Photosynthetic ability in terms of CO_2 exchange rate has been studied by several authors and was found to be higher in F_1 hybrids by some authors (Murayama et al., 1987 ; Khan et al., 1997).

However, others did not find any heterosis for this trait (Kabaki et al., 1976).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). Carbon assimilation during the grain filling period is specifically important because 60$\sim$100% of carbon for grain filling comes from carbon assimilated during the grain filling period (Yoshida, 1981). Thus the post anthesis photosynthetic efficiency is of immense importance for grain yield production in rice. Improvement in yield in F_1 hybrids might be possible by modifying the panicle geometry and by improving the individual components of the panicle through favourable hybridization. Here we discussed some of the important factors that might influence the yield capability, especially those related to the post anthesis photosynthetic ability of F_1 hybrids in rice.

Materials and Methods

1. Plant Growing

F_1 hybrid seeds were produced during the second growing season of 1995 by crossing parental cultivars Akebono, Chiyonishiki and Zenith. Akebono and Chiyonishiki are semidwarf japonica cultivars, but Zenith is a tall American variety also of japonica type.

Corresponding author : M.N.A. Khan (nurulkhan@hotmail. com).

Chiyonishiki is commercially cultivated in Okinawa prefecture. F_1 cross combinations of Akebono × Chiyonishiki (semidwarf × semidwarf) and Zenith × Akebono (tall × semidwarf) were used for the present study. The experiment was carried out in the glass house of the Faculty of Agriculture (University of the Ryukyus), Okinawa, Japan (26° 10′ N and 127° 45′ E).

Seeds of parent cultivars and F_1 hybrids were treated with systemic fungicide "Benelet T" and were sown in nursery boxes (60 × 35 × 8 cm) on the soil medium on 01 March, 1996. Three-week-old seedlings of each parental cultivar and F_1 hybrids were transplanted individually in the 0.02 m² Wagner pot containing Shimajiri Mahji (Dark Reddish) Soil distributed in the Okinawa region. Soils in the pot were mixed with organic matter at the rate of 3 kg per m² and puddled in order to mimic natural wetland paddy field condition. Inorganic fertilizers were supplied, as basal application, according to the recommended dose for the first growing season in Okinawa region at the following rates : N, 6.5 g m⁻² ; P_2O_5, 5 g m⁻² ; K_2O, 6.0 g m⁻². First top dressing of NPK fertilizers was made at 50 days after sowing around the panicle initiation stage at the following rate : N, 3.5 g m⁻² ; P_2O_5, 2.5 g m⁻² ; and K_2O, 3.0 g m⁻². Second top dressing of the inorganic fertilizers were done 85 days after sowing at the following rate : N, 3.0 g m⁻² ; P_2O_5, 2.5 g m⁻² ; K_2O, 3.0 g m⁻². Plants were watered daily so that the plants remained in at least 5 cm of standing water throughout the trial. The glass house was kept well ventilated to maintain a natural temperature and light condition inside the glass house. To avoid the border effect the variety Akebono was planted as guard rows. The crop was free from insect and disease infestation. However, as a precautionary measure Diazinon (granular) was applied 45 days after sowing.

2. Measurements

Six destructive samplings had been done commencing from two months after sowing. Plant height was measured as the length from the base to the tip of the leaf or the panicle whichever was greater. Leaf area was measured with an automatic area meter (AAM, Hayashi Denko, Japan) immediately after harvest to avoid shrinkage and leaf rolling. Dry weight was measured after drying the plants at 80°C for 48 hours in an oven. At the final harvest, yield and several characters contributing to yield were assessed. Grain yield was measured at maturity after threshing, cleaning, and drying. The number of panicles on four plants were counted, and three panicles from each plant were randomly selected for counting the number of spikelets per panicle, fraction of unfilled spikelets and hundred seed weight. Important panicle characteristics, e.g., panicle length, the number of primary branches per panicle, the mean number of spikelets per primary branch and the mean length of primary branches were also recorded for three randomly selected panicles from the F_1 hybrids and parent cultivars.

Carbon dioxide exchange rate (CER) was measured at 55 days after sowing at the panicle initiation stage and again at 112 days at the flowering stage with a portable infra-red CO_2 gas analyzer and Parkinson leaf chamber. Three 1000 W halogen lamps were used to maintain a light intensity of 1000 μ moles m⁻² sec⁻¹ during the assessment period. The atmospheric air flow rate was adjusted to 400 ml per minute inside the chamber, using an Asum-2 air supply unit. Three plants from each of the parent cultivars and F_1 hybrids were randomly selected for CER assessment. The two topmost fully expanded leaves were used and three readings were taken from each leaf. The means of these readings were used for comparing the F_1 hybrids and parental cultivars.

Heterosis was assessed as the value of F_1 hybrid/mid parental value, where the mid-parental value was the mean of the values of the parents. Data were analyzed by the Analysis of Variance (ANOVA) technique and means were tested by the least significance difference (LSD) test. Statistical analyses were done following the procedure laid out in Clewer and Scarisbrick (1990) and Gomez and Gomez (1984).

Results

In both the hybrid combinations of Zenith × Akebono (Z × A) and Akebono × Chiyonishiki (A × C) the F_1 hybrid was taller than the respective better parent (Table 1). Heterosis for Z × A (1.17) was higher than that for A × C (1.03). The average heterosis for plant height was 1.10 for the two parental combinations. The number of tillers per plant in the F_1 plants was higher than that in the better parent in A × C, but was lower than the mid parental value in Z × A (Table 1). The average heterosis was 1.01 for the number of tillers per plant.

Leaf area per plant in the F_1 hybrid of A × C was larger than that in either parent throughout the growing season, and the differences were significant during pre-heading growth stages (Fig. 1a). However, at the post-anthesis growth stages the differences between F_1 hybrid and parents were slight. In Z × A, the leaf area in the F_1 hybrid was significantly larger than that in either parent during the pre-heading earlier growth stages but, with the onset of flowering a rapid decline was observed in the F_1 plants (Fig. 1b). Leaf area in the F_1 hybrid of this parental combination was slightly smaller than that in either parent at the post-heading growth stages.

Dry matter (DM) accumulation in the F_1 plants in A × C was greater than that in the parent cultivars throughout the growing season (Fig. 2a). On the contrary, in the F_1 hybrid of Z × A although the DM accumulation was significantly greater than that of the parent cultivars at early growth stages, it was similar to, or even less than that of parent cultivars after onset of flowering (Fig. 2b). DM accumulation in the F_1 hybrid of this parental combination at the final harvest was less than the

Table 1. Plant height and number of tillers per plant in the F₁ hybrids and parent cultivars.

Parental combination		Female parent	F₁ hybrid	Male parent		LSD (5%)	Heterosis
Akebono × Chiyonishiki	Plant height (cm)	113.1	114.5	110.0	ns	10.67	1.03
	Number of tillers per plant	13.0	13.5	10.8	ns	2.37	1.13
Zenith × Akebono	Plant height (cm)	153.7	156.3	113.1	**	12.73	1.17
	Number of tillers per plant	6.0	8.5	13.0	**	2.07	0.89
			Average heterosis	Plant height			1.10
				Number of tillers per plant			1.01

Ns and ** indicate statistically nonsignificant and significant at the 1% level respectively.
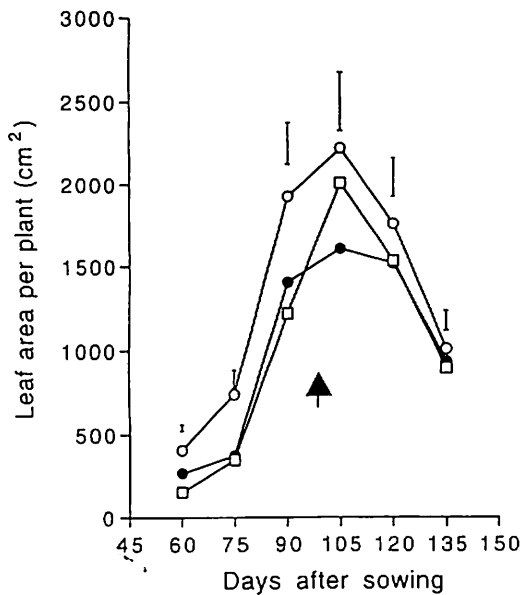Heterosis was calculated as value of F₁ hybrid/mid-parental value.

Fig. 1a. Change in leaf area with time in F₁ hybrids and inbred parent cultivars (Akebono × Chiyonishiki).
—□— Akebono ; —●— Chiyonishiki ; —○— Akebono × Chiyonishiki. Bars represent LSD at the 5% level of significance. Arrow indicates time of heading.
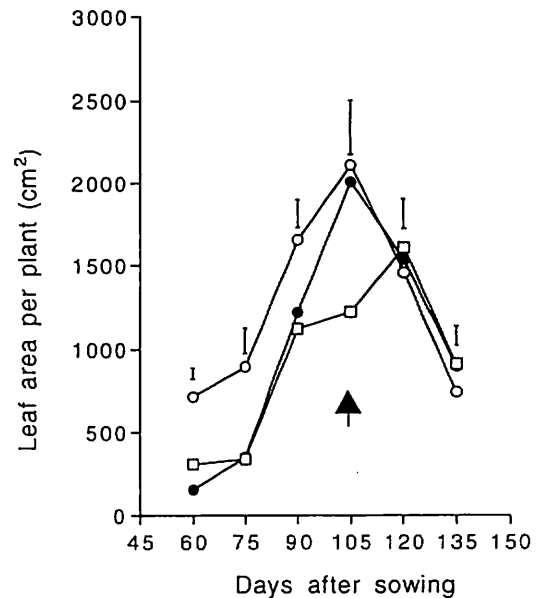

Fig. 1b. Change in leaf area with time in F₁ hybrids and inbred parent cultivars (Zenith × Akebono).
—□— Zenith ; —●— Akebono ; —○— Zenith × Akebono. Bars represent LSD at the 5% level of significance. Arrow indicates time of heading.

mid-parental value.

The CO₂ exchange rate (CER) in all the parental cultivars and F₁ hybrids decreased with time and it was higher at the panicle initiation stage than at the flowering stage (Table 2). No significant difference in CER was observed among parent cultivars and between F₁ hybrids and parent cultivars in either stage. In A × C, CER in the F₁ hybrid was higher than the mid-parental value at the panicle initiation stage, heterosis at this stage was 1.05 but lower than the mid-parental value at the flowering stage (heterosis, 0.91). In Z × A, CER at either

stage was lower than the mid-parental value and the degree of heterosis was much lower at the flowering stage (0.84) than at the panicle initiation stage (0.94).

Various characters contributing to yield are shown in table 3. The number of panicles per plant was higher than that in the better parent in A × C, and was lower than the mid-parental value in Z × A. The number of spikelets per panicle in the F₁ hybrids of both parental combinations was higher than the respective better parent. The percentage of unfilled spikelets in the F₁ hybrid was higher than that in either parent in both
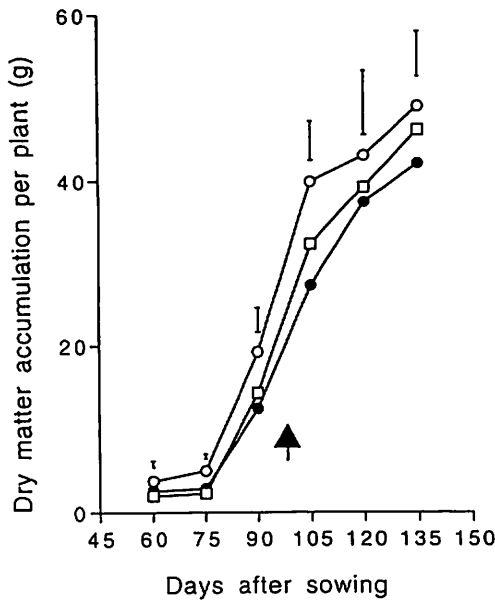
Fig. 2a. Change in dry matter accumulation in F_1 hybrids and inbred parent cultivars (Akebono × Chiyonishiki).
—□— Akebono ; —●— Chiyonishiki ; —○— Akebono × Chiyonishiki. Bars represent LSD at the 5% level of significance. Arrow indicates time of heading.
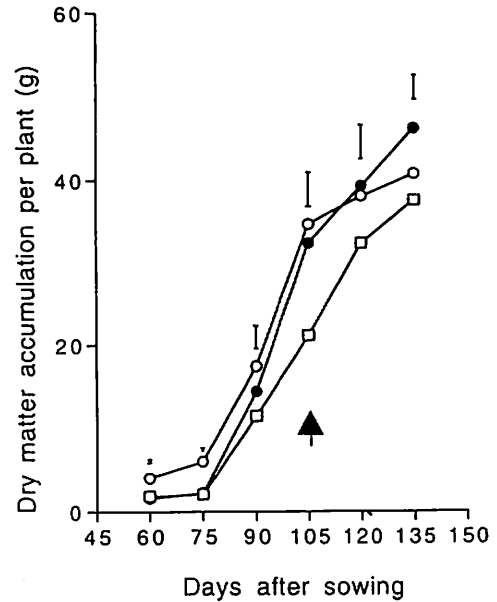
Fig. 2b. Change in dry matter accumulation in F_1 hybrids and inbred parent cultivars (Zenith × Akebono).
—□— Zenith ; —●— Akebono ; —○— Zenith × Akebono. Bars represent LSD at the 5% level of significance. Arrow indicates time of heading.

Table 2. Carbon dioxide exchange rate (CER) at panicle initiation stage and at flowering stage of the F_1 hybrids and parent cultivars.

Parental Combination	Growth stage	CER (μ moles m^{-2} sec^{-1})					Heterosis
		Female parent	F_1 hybrid	Male parent		LSD (5%)	
Akebono × Chiyonishiki	Panicle initiation	21.16	23.80	24.11	ns	6.89	1.05
	Flowering	18.02	16.80	18.94	ns	3.73	0.91
Zenith × Akebono	Panicle initiation	19.18	18.94	21.16	ns	4.31	0.94
	Flowering	15.34	13.99	18.02	ns	5.76	0.84

Ns represents statistically nonsignificant. For heterosis see footnote of Table 1.

parental combinations the difference being much higher in the case of Z × A (24.9 %). The 100 seed weight in the F_1 hybrid was slightly lower than the respective mid-parental weight in both parental combinations (Table 3).

Table 4 shows the characteristics of several important panicle components. Panicle length in the F_1 plants was similar to that of the mid-parental length in A × C, but was longer than that of the better parent in Z × A, the degree of heterosis was as high as 1.25. The number of primary branches per panicle and the mean lengths of the primary branches in the F_1 hybrids were greater than the mid-parental values in both parental combinations. The mean number of spikelets per primary branch of the F_1 hybrids was higher than that of the rspective better parent in both parental combinations. High heterosis in this respect was observed in both parental combinations.

In the parental combination A × C, both the grain

yield per plant and harvest index in the F_1 hybrid was higher than those in the better parent. On the contrary, in the parental combination of Z × A the grain yield per plant and harvest index in the F_1 hybrid were lower than the mid-parental values. Average heterosis in grain yield and harvest index were 1.03 and 0.98 respectively.

Discussion

Singh et al. (1980) reported a positive heterosis in plant height in rice, and the same was also the case in our experiments. Virmani (1994) reported that positive heterosis in height is common in rice although there are a few instances of negative heterosis (Singh and Singh, 1978). Positive heterosis in plant height is not desirable because plant height is negatively correlated with lodging resistance (Chang, 1967). Most of the modern high yielding rice cultivars are dwarf or semi-dwarf plants having lodging resistance and facilitating better radiation

Table 3. Comparison of the yield contributing characters between F₁ hybrids and parental cultivars.

Parental Combination	Yield character	Female parent	F₁ Hybrid	Male parent		LSD (5%)	Heterosis
Akebono×Chiyonishiki	Number of panicles/plant	12.0	13.0	10.0	ns	2.72	1.18
	Number of spikelets/panicle	114.3	135.5	125.0	*	14.97	1.13
	Percent of unfilled spikelets (%)	13.2	14.7	10.3	ns	4.06	—
	100 seed weight (g)	2.24	2.15	2.23	*	0.07	0.96
Zenith×Akebono	Number of panicles/plant	6.0	8.0	12.0	**	2.11	0.89
	Number of spikelets/panicle	154.5	167.8	114.3	**	14.75	1.25
	Percent of unfilled spikelets (%)	17.9	24.9	13.2	**	5.51	—
	100 seed weight (g)	2.08	2.05	2.24	**	0.10	0.95

Average heterosis : Number of panicles/plant 1.04
Number of spikelets/panicle 1.19
100 seed weight 0.96

Ns, * and ** indicate statistically nonsignificant and significant at the 5% and 1% level respectively. For heterosis see footnote of Table 1.

Table 4. Important panicle characteristics of F₁ hybrids and parent cultivars.

Perental combination	Panicle characteristic	Female parent	F₁ hybrid	Male parent		LSD (5%)	Heterosis
Akebono×	Panicle length (cm)	20.8	21.4	22.2	ns	2.61	0.99
Chiyonishiki	Number of primary branches/panicle	8.2	8.8	8.7	ns	1.75	1.04
	Mean length of primary branches (cm)	8.3	9.1	8.8	ns	1.34	1.06
	Mean number of spikelets/primary branch	13.1	16.6	15.0	**	1.79	1.18
Zenith×	Panicle length (cm)	30.8	32.2	20.8	**	3.16	1.25
Akebono	Number of primary branches/panicle	10.7	10.5	8.2	*	1.90	1.11
	Mean length of primary branches (cm)	10.9	10.3	8.3	*	1.82	1.07
	Mean number of spikelets/primary branch	16.7	17.5	13.1	**	2.68	1.17

For symbols see footnotes of Tables 1 and 3.

penetration into the canopy. Heterosis in number of tillers varied with the parental combination. The F₁ hybrid of the parental combination A × C, a combination of the cultivars having similar and high tillering ability manifested high positive heterosis. However, the F₁ hybrid of Z × A, a combination of the cultivars having a great difference in number of tillers expressed rather negative heterosis. In a previous study with 16 F₁ hybrids, similar results have been observed (Khan et al., 1997). Govinda Raj and Siddiq (1986) observed a positive heterosis in this trait but Virmani et al. (1981) reported a negative heterosis in the number of tillers per plant.

The visually observed leaf area in the F₁ hybrids was larger than that in either parent from the seedling stage. Post-heading rapid decline in leaf area might be caused by the reduction in leaf nitrogen content and radiation penetration into the canopy in the F₁ hybrids. Rice is a determinate crop and with the onset of flowering leaf senescence starts and the inflorescence cuts a consider-

Table 5. Grain yield and harvest index of F_1 hybrids and parent cultivars.

Parental combination		Grain yield per plant (g) and harvest index (HI)					
		Female parent	F_1 hybrid	Male parent		LSD (5%)	Heterosis
Akebono× Chiyonishiki	Grain yield	18.9	22.2	18.2	**	2.24	1.19
	HI	0.41	0.45	0.44	ns	0.06	1.06
Zenith× Akebono	Grain yield	13.9	14.3	18.9	**	1.90	0.87
	HI	0.37	0.35	0.41	ns	0.06	0.90
		Average heterosis		Grain yield			1.03
				HI			0.98

For symbols see footnote of Tables 1 and 3.

able amount of photosynthetically active radiation (PAR) to enter into the canopy. Murata et al. (1968) observed that panicle removal increased 13～20% PAR penetrating into the canopy. Kabaki et al. (1976) stated that the leaves of the F_1 plants had a lower nitrogen content than the parent cultivars due to higher leaf area in the F_1 plants. Decline in leaf area in F_1 plants was much greater in Z × A than in A × C. The F_1 hybrid of Z × A was taller and had longer panicles than A × C (Table 4). Thus PAR penetrating into the canopy might be reduced to a greater extent in the former. During the grain filling stage one of the major effects of the developing panicles in rice is the shading of leaves because of upper positioned panicles over the canopy. Setter et al. (1995) showed that in a crop yield of 6-7 ton ha^{-1} the panicle covered 0.45～0.90 m^2 m^{-2}. Murata et al. (1968) suggested that shading of the leaves by the growing panicles were mainly responsible for the reduced crop growth rate (CGR) during grain filling. Canopy architecture of the F_1 hybrid of Z × A during the grain filling stage was not desirable because almost all the leaves supposed to supply photo-assimilate to the panicle were beneath the long curved panicles and consequently at a much lower irradiance. On the contrary, the panicles in the F_1 hybrid of A × C were somewhat erect and short. Wenfu et al. (1995) reported that a cultivar with erect panicles had about 10% higher growth rate and a 15% greater yield compared to a cultivar with a curved panicle. Setter et al. (1996) mentioned that reduced panicle height in a rice crop canopy had a beneficial effect in increasing yield potential through reduced shading leading to a greater canopy photosynthesis. These authors observed that canopy photosynthesis in rice plants with shorter panicles is greater than that in the plants with longer panicles, even when the single leaf photosynthesis was similar.

The lower DM accumulation at later growth stages in the F_1 plants of Z × A might be due to a reduction in crop's photosynthetic ability in terms of leaf area and CER. Khan et al. (1997) reported a high correlation between heterosis in leaf area and heterosis in dry matter

accumulation in rice. Gallagher and Biscoe (1978) mentioned that under favourable conditions dry matter accumulation in the cereals was proportional to the amount of radiation they intercepted.

Decrease in CER with age was more conspicuous in the F_1 plants than in the parental cultivars. This caused a lower degree of heteroses in CER at the flowering stage than at the panicle initiation stage in both hybrids. The comparatively lower (compared to mid-parental value) CER at flowering stage in the F_1 hybrids might be caused by a lower nitrogen content in the leaves of the F_1 hybrids. Sinclair and Horie (1989) mentioned that a higher nitrogen content in the leaf increased photosynthetic rates and radiation use efficiency. The activity of photosynthetic enzymes such as rubisco activity is also a major determinant of CER. The variations in the heterosis results for CER among different authors could be attributed to the difference in nitrogen content and growth stages at which they were examined.

In both parental combinations, the number of spikelets per panicle in the F_1 hybrid was higher than that of the respective better parent. In Z × A, however, the overall grain yield per plant was lower than that of the mid-parental yield because of fewer panicles per plant and higher percentage of unfilled grains. Murayama et al. (1974) and Singh and Singh (1978) reported that both the number of panicles per plant and spikelets per panicle contributed to higher grain yield in the F_1 hybrid. The results of the present experiment are in agreement with theirs. On the contrary, Ponnuthurai et al. (1984) stated that heterosis in grain yield of F_1 rice hybrid was mainly caused by the increase in the number of spikelets per panicle, and that the number of panicles per plant did not significantly contribute to the heterosis in grain yield. Due to reduced photosynthetic ability, the F_1 plants of Z × A, might not be able to provide the necessary amount of photoassimilates to a large number of spikelets set producing a higher fraction of unfilled grains. Thus no heterosis in grain yield might be achieved in this hybrid combination. In other words the panicle geometry was not efficient in the F_1 hybrid of

Z × A. Probably, the plants with a short and erect panicle containing a higher number of spikelets without having much shading effect have a better yield.

Grain yield in the F₁ plants was closely associated with the harvest index. High heterosis in grain yield in A × C was associated with high heterosis in harvest index, and a low heterosis in grain yield in Z × A was associated with low heterosis in harvest index. In modern high yielding cereal cultivars seed yield was primarily increased by the increase in harvest index (Walsh, 1984). Ponnuthurai et al. (1984) reported a positive heterosis in harvest index for F₁ hybrid plants, but our results were not in full agreement with theirs.

In the present study, high pre-anthesis higher dry matter accumulation caused the production of a large number of spikelets. However, due to reduced post-anthesis photosynthetic ability, heterosis in grain yield was not achieved in Z × A. On the contrary, high pre-anthesis dry matter accumulation as well as somewhat better post-anthesis photosynthetic ability resulted in positive heterosis in grain yield in A × C. Although F₁ hybrids derived from tall parents with a small number of tillers per plant, such as Zenith, seemed to have developed a high yield potential through high dry matter accumulation at an early vegetative growth stage, they finally did not show heterosis in the yield due to low post-anthesis photosynthetic efficiency. Post-anthesis crop photosynthesis is an essential factor to gain a high yield in rice. Therefore, tall cultivars should be excluded as parents at the time of breeding for F₁ hybrids. Top dressing of nitrogen fertilizer at later growth stages (post-anthesis) might be helpful for increasing the crop photosynthesis at these stages. Further studies giving different levels of nitrogen fertilizer at different growth stages, particularly at the post anthesis growth stages under field conditions are needed to obtain more practical information in exploiting the yield potential of the F₁ hybrids in rice.

References

Chang T.T. 1967. Growth characteristics, lodging and grain development. Int. Rice Comm. Newsl. (Special issue) : 54—60.

Clewer A.G. and Scarisbrick D.H. 1990. An Introduction to the Principles of Crop Experimentation. Wye College (University of London), London. 1—93.

Gallagher J.N. and Biscoe P.V. 1978. Radiation absorption, growth and yield of cereals. J. Agric. Sci. Camb. 91 : 47—60.

Gomez K.A. and Gomez A.A. 1984. Statistical Procedure for Agricultural Research. Second edition. John Wiley and Sons Inc., New York. 1—680.

Govinda R.K. and Siddiq E.A. 1986. Hybrid vigour in rice with reference to morphophysiological components of yield and root density. SABRAO J. 18 : 1—7.

Jennings P.R. 1967. Rice heterosis at different growth stages in tropical environment. Int. Rice Comm. Newsl. 16 : 24—26.

Kabaki N., Akita S., Tanaka I. and Amamiya A. 1976. Photosynthesis and photorespiration of cultivated rice and F₁ hybrid. Proc. Crop Sci. Soc. Japan 45 (Extra issue 2) : 177—178*.

Kawano K., Kurosawa S. and Takahashi M. 1969. Heterosis in vegetative growth of the rice plant. Genetical studies on rice plants. Japan. J. Breed. 19 : 335—342.

Khan M.N.A., Murayama S., Ishimine Y., Tsuzuki E. and Nakamura I. 1997. Physio-morphological studies of F₁ hybrids in rice (Oryza sativa L.). I. Heterosis in characters related to matter production. Jpn. J. Crop Sci. 66 (Extra issue 2) : 66—67.

Kropff M.J., Cassman K.G., Peng S., Matthews R.B. and Setter T.L. 1994. Quantitative understanding of rice yield potential. In K.G. Cassman ed., Breaking the Yield Barrier. Proc. Workshop on Rice Yield Potential in Favourable Environments. IRRI, Los Banos. 21—38.

Lin S. C. and Yuan L.P. 1980. Hybrid rice breeding in China. In Innovative Approaches to Rice Breeding. Selected Papers from the 1979 International Rice Research Conference. IRRI, Los Banos. 35—51.

Murata Y., Miyasaka A., Munakata K. and Akita S. 1968. On the solar energy balance of rice population in relation to the growth stage. Proc. Crop Sci. Soc. Japan 37 : 685—691**.

Murayama S., Miyazato K. and Nose A. 1987. Studies on matter production of F₁ hybrid in rice. Heterosis in the single leaf photosynthetic rate. Jpn. J. Crop Sci. 56 : 198—203.

Murayama S., Omura T. and Miyazato K. 1974. Basic studies on utilization of hybrid vigour in rice. Heterosis under different cultural conditions. Japan. J. Breed. 24 : 287—290.

Ponnuthurai S., Virmani S.S. and Vergara B.S. 1984. Comparative studies on the growth and grain yield of some F₁ rice (Oryza sativa L.) hybrids. Phillip. J. Crop Sci. 9 : 183—193.

Setter T.L., Conocono E.A. and Edgane J.A. 1996. Possibility of increasing yield potential of rice by reducing panicle height in the canopy. II. Canopy photosynthesis and yield of isogenic lines. Aust. J. Plant Physiol. 23 : 161—169.

Setter T.L., Conocono E.A., Edgane J.A. and Kropff M.J. 1995. Possibility of increasing yield potential of rice by reducing panicle height in the canopy. I. Effects of panicles on light interception and canopy photosynthesis. Aust. J. Plant Physiol. 22 : 441—451.

Sinclair T.R. and Horie T. 1989. Leaf nitrogen, photosynthesis and crop radiation use efficiency : a review. Crop Sci. 29 : 90—98.

Singh S.P. and Singh H. G. 1978. Heterosis in rice. Oryza 15 : 173—175.

Singh S.P., Singh R.P. and Singh R.V.1980. Heterosis in rice. Oryza 17 : 109—113.

Virmani S.S. 1994. Heterosis and Hybrid Rice Breeding. Springer-Verlag, London. 1—189.

Virmani S.S., Chaudhary R.C. and Khush G.S. 1981. Current outlook on hybrid rice. Oryza 18 : 67—84.

Walsh E.N. 1984. Developing yield potential of cereals. In E.J. Gallagher ed., Cereal Production. Butterworth, London. 69—93.

Wenfu C., Zhengjin X., Longbu Z., Hongfei Z. and Shouren Y. 1995. Effects of different panicle type on canopy properties, light distribution and dry matter production of rice population. Acta Agron. Sin. 21 : 83—89.

Yoshida S. 1981. Fundamentals of Rice Crop Science. IRRI, Los Banos. 1—269.

*In Japanese.Translated by the present authors.
**In Japanese with English summary.