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Growth and Yield of Japonica-Indica Hybrid Rice

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Abstract
Japonica-Indica hybrid rice lines produced tillers vigorously during the 30-day period after transplanting and exhibited a high degree of heterosis in terms of crop growth rate (CGR). Though the degree of heterosis decreased thereafter, it rose again after heading, contributing to the good characteristics of maturation in hybrid rice. High yield of hybrid rice lines was attained by the summation of the increase of each yield component. Response of hybrid rice to fertilizer was distinctive with the enhancement of both dry matter production and yield associated with the large amount of fertilizer applied. Tolerance to unfavorable environments such as low temperature and low light intensity was higher than that of the parental varieties at the vegetative stage, whereas at the reproductive stage it was lower than that of Japonica varieties. Thus, the Japonica-Indica hybrid rice lines appear to have the potential to achieve a superhigh yield in the northern region of Japan.

Discipline: Crop production
Additional key words: dry matter production, plant breeding, tolerance to environment

Introduction

Hybrid rice is a promising material for producing superhigh yields in rice, through the utilization of the hybrid vigor generated when diverse parental varieties are hybridized. Selection of the parental varieties is most important to attain a high yield in hybrid rice and much effort has been devoted to identify varieties with a high combining ability. The efficiency of research could be enhanced if standards of selection could be established based on information on the eco-physiological traits of classified varieties. The current studies aimed at clarifying the characteristics of Japonica-Indica hybrid rice lines with reference to dry matter production, yield and tolerance to unfavorable environmental conditions. Research was conducted over a period of three years (1989-1991) in a field consisting of clayey gley soil located at the Hokuriku National Agricultural Experiment Station.

Materials

Japonica-Indica hybrid rice lines were developed in the Laboratory of Plant Breeding Methodology by crossing cytoplasmic male sterile (CMS) lines and semidwarf Indica varieties. CMS lines bore the cytoplasm of Chinsurah Boro II and the nucleus of the Japonica varieties Akihikari (MS1003) or Nekken 2 (MS(N)). Paternal Indica varieties included Milyang 23, JiaNongXian 11, XinQingAi 1, Reakyung, IR 24 and Suwon 258. Growth and yield of the hybrid rice lines were characterized by comparing individual varieties (combinations) and three groups, i.e. Japonica (Akihikari, Nekken 2, Fujisaka 5 and Kinuhikari), Indica (mentioned above) and hybrid rice lines.

Dry matter production of Japonica-Indica hybrid rice

Heterosis of hybrid rice was examined throughout

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the growth period by the analysis of dry matter production.

Hybrid rice lines were not superior to the parental varieties in the initial period of growth from germination until the young seedling stage of 3-leaf age (Fig. 1). However, they produced tillers vigorously during the 30-day period after transplanting, which resulted in the highest crop growth rate, expressed by the rate of increase in dry weight. Though the increase of the tiller number in the hybrid rice lines slowed down thereafter and even decreased markedly before heading, the crop growth rate remained high in this period. After heading, the crop growth rate of the hybrid rice lines was higher than that of the parental varieties and contributed to the increase of panicle weight with a ratio of more than 80% in hybrid rice. Crop growth rate of Indica varieties declined after heading and the rate of contribution to panicle weight remained at around 60%, indicating their dependence on translocation from straw (Table 1).

Changes due to heterosis in the parameters of growth analysis are shown in Fig. 2. Heterosis in leaf area index (LAI) was highest in the initial 30-day period after transplanting and thereafter it gradually

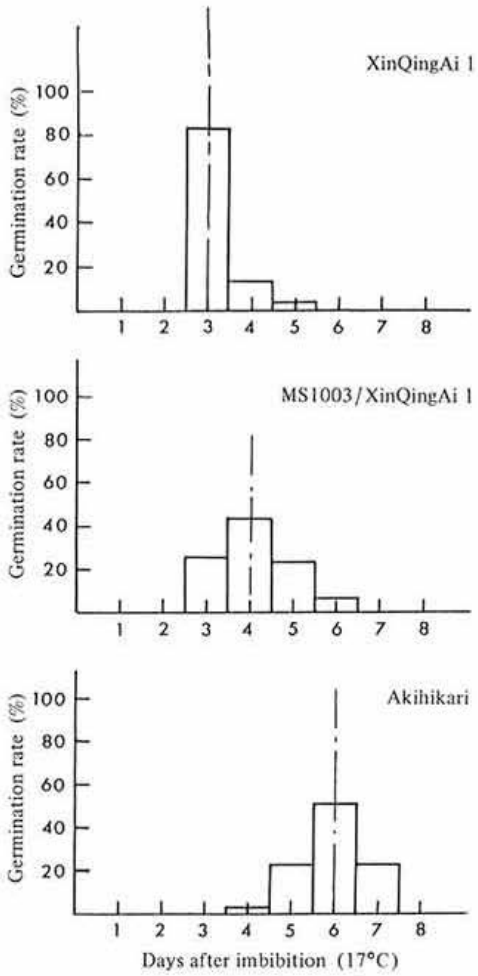

Fig. 1. Time course of germination
MS1003: Male sterile line with the nucleus of Akihikari.

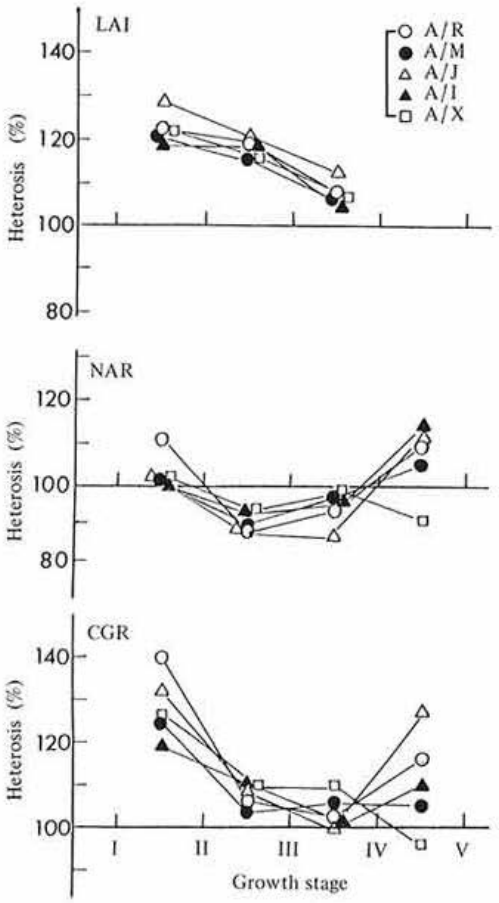

Fig. 2. Changes in the degree of heterosis in the parameters of growth analysis
Materials: A; Male sterile line with the nucleus of Akihikari, R; Reakyung, M; Milyang 23, J; JiaNongXian 11, I; IR 24, X; XingQingAi 1.
Growth stage: I; Transplanting, II; 30 DAT, III; 60 DAT, IV; Heading, V; Harvest.

Table 1. Characteristics of growth in three groups of varieties (lines)

	Growth stage[d]	Japonica[a]		Indica[b]		Hybrid[c]	
		1989	1990	1989	1990	1989	1990
Growth duration		144	139	155	151	144	141
Rate of increase in tiller number ($/m^2 \cdot day$)	I	8.90	6.92	12.58	9.01	14.76	11.87
	II	5.03	4.67	7.32	8.41	2.47	3.85
	III	-4.00	-2.26	-8.58	-8.25	-12.73	-11.63
Rate of increase in leaf area ($cm^2/m^2 \cdot day$)	I	281	151	386	236	500	278
	II	1,509	985	1,639	1,242	1,664	1,367
	III	591	510	843	563	762	436
Rate of increase in dry weight ($g/m^2 \cdot day$)	I	2.79	1.45	2.94	1.77	4.29	2.20
	II	13.78	10.84	14.43	11.58	17.19	13.58
	III	24.70	31.43	24.20	30.17	25.72	32.06
	IV	14.83	17.40	12.89	14.89	17.91	17.78
	I~IV	12.60	12.95	13.46	13.76	15.18	14.57
Ratio of increase[e] (Total/Panicle: %)		85.1	98.2	62.7	64.0	93.0	81.1

a): Japonica; Akihikari, Kinuhikari, Fujisaka 5 (1989).
Akihikari, Kinuhikari, Nekken 2 (1990).
b): Indica ; Milyang 23, JiaNongXian 11, XinQingAi 1, Reakyung.
c): Hybrid ; CMS line with nucleus of Akihikari/Indica (1989).
CMS line with nucleus of Nekken 2/Indica (1990).
d): Growth stage; I; 30 days after transplanting (DAT), II; 30-60 DAT, III; 60 DAT-Heading (20-40 days), IV; Heading-Harvest (35 days), I-IV; Transplanting-Harvest.
e): Ratio of increase; (Increase of total dry weight after heading/ Increase of panicle weight after heading) × 100.

Table 2. Yield and yield components in 3 groups of varieties (lines)

Group of varieties (lines)	Panicle no. ($/m^2$)	Spikelet no. per panicle	Spikelet no. ($\times 100/m^2$)	Percentage of ripened grains (%)	1000 Grain weight (g)	Brown rice yield (kg/10 a)
Japonica	381±34	97±14	370±49	79±11	21.6±0.8	608±70
Indica	344±46	126±18	431±69	76±11	21.9±2.2	700±83
Hybrid	361±31	136±11	488±60	67± 7	22.8±1.4	736±53

Each group was composed of 4 varieties (lines).
Data were expressed by mean±S.D. from the field trials for three years (1989-1991).

decreased. Net assimilation rate (NAR) of hybrid rice was almost the same as that of the mid-parents at the initial stage. It declined until heading and rose again after heading. Decrease of NAR at the middle stage was attributed to mutual shading of leaves due to the vigorous growth of the hybrid rice lines. There were no differences in the photosynthetic activity per unit leaf area between hybrid rice lines and the parental varieties. The increase of NAR after heading was due to the decrease in the activity of the leaves in the paternal Indica varieties. The change of the crop growth rate (CGR) showed the same pattern as that of NAR but always exceeded the level of that of the mid-parents. Thus, hybrid rice was characterized by vigorous growth at the initial vegetative stage followed by the persistence of a high dry matter production throughout the reproductive stage.

Yield and yield components of Japonica-Indica hybrid rice lines

Since rice is a kind of grain crop, its production depends on both biological (dry matter) production and efficiency of grain production. The characteris-

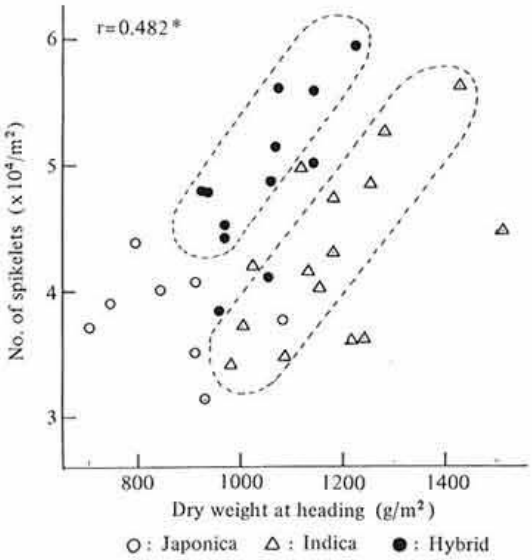

Fig. 3. Relationship between dry weight at heading and no. of spikelets

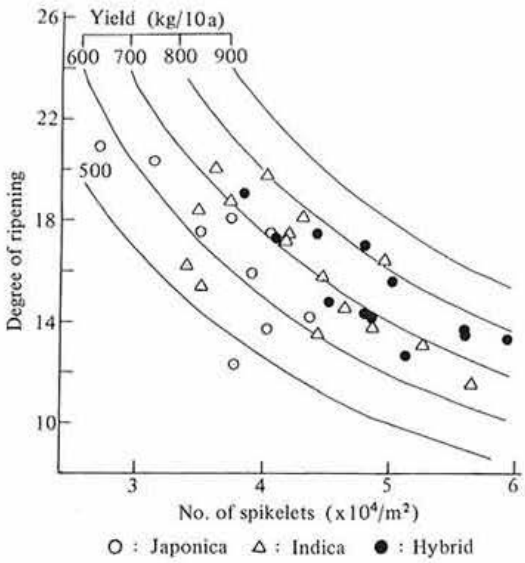

Fig. 4. Relationship between no. of spikelets and degree of ripening
Degree of ripening: Ripening percentage × 1000 grain weight.

tics of grain production of hybrid rice were represented in the relationship with dry matter production.

Hybrid rice lines exhibited high yields due to the summation of the increase of each yield component (Table 2). The number of panicles per unit area was intermediate between that of the parental varieties while the number of spikelets per panicle exceeded that of the parents. As a result, the number of spikelets per unit area was highest in the hybrid rice lines. The percentage of ripened grains in hybrid rice was low due to hybrid sterility while the 1000 grain weight was high. Thus, the combination of these yield components resulted in high yields of hybrid rice (700–800 kg/10 a in brown rice) with a high degree of heterosis (110–125%) throughout the field trials for three years.

Grain formation in the hybrid rice lines was more efficient than that of the parental varieties based on dry matter production (Fig. 3) and the high dry matter production of hybrid rice after heading contributed to the relatively high degree of ripening with the larger number of spikelets (Fig. 4).

Effects of fertilizer application on dry matter production and yield in hybrid rice lines

Application of fertilizer affected the dry matter production and yield differently in the three groups of varieties or lines (Table 3). Increase of total dry weight with fertilizer application was highest in the hybrid rice lines. Though the rate of increase in dry weight with fertilizer application was high until heading in Indica varieties, it decreased after heading reflecting the low dry matter production after

Table 3. Effects of fertilizer application on dry matter production and yield in 3 groups of varieties (lines)

	Ratio[a] (Applied/Not applied: N_{12}/N_0)		
	Japonica	Indica	Hybrid
Dry weight at heading	1.49	1.68	1.66
Increase of dry weight after heading	1.59	1.26	1.59
Total dry weight at harvest	1.53	1.55	1.64
Spikelet no. per m^2	1.91	1.65	1.93
Degree of ripening[b]	0.89	0.83	0.93
Brown rice yield	1.69	1.36	1.83

a): Fertilizer application: Nitrogen 12 kg /10 a (N_{12}) versus 0 kg/10 a (N_0).
b): Degree of ripening: Percentage of ripened grains × 1000 grain weight.

heading. Increase of yield with fertilizer application was also highest in the hybrid rice lines due to the increased number of spikelets and relatively higher degree of ripening. Thus, hybrid rice exhibited a higher yield potential with the application of large amounts of fertilizer.

Tolerance to unfavorable environments in hybrid rice lines

Tolerance to unfavorable environments, such as low temperature (16–18°C) or low light intensity (50% shading), was examined at both the vegetative and reproductive stages. Vegetative growth of the hybrid rice lines was least inhibited by low temperature or shading and the degree of heterosis increased under these conditions (Table 4). Growth of Indica varieties was seriously impaired at a low temperature and leaves displayed symptoms of chlorosis.

Hybrid rice lines were more tolerant to low temperature damage at the pollen reduction division stage than the paternal Indica varieties (Fig. 5). However, the tolerance was inferior to that of the Japonica varieties. Shading treatment at the heading stage caused a high percentage of sterility in the hybrid rice lines.

Discussion

Heterosis in hybrid plants has been attributed to the "early starter" phenomenon, including faster germination. Akita et al.[2] reported the superiority of initial growth in Indica–Indica hybrid rice which resulted from a larger embryo size and higher growth

Table 4. Effects of low temperature and shading treatments on growth at the tillering stage in 3 groups of varieties (lines)

Growth traits	Relative rate of growth[a] (percentage of control)						Heterosis[d]		
	Low temperature[b]			Shading[c]					
	Japonica	Indica	Hybrid	Japonica	Indica	Hybrid	Control	Low temp.	Shading
Plant height	80	59	74	106	196	103	107	113	109
No. of panicles	43	35	55	54	56	59	96	134	103
Leaf area	26	16	30	58	55	62	124	180	138
Shoot dry weight	33	21	33	45	42	49	137	166	155
Root dry weight	32	18	30	36	38	41	162	200	181
Total dry weight	32	21	32	43	41	48	141	172	159

a): (Growth under low temperature or shading/control) × 100.
b): 18°C for 28 days at 6-leaf age.
c): 50% shading with cheese cloth for 28 days at 6-leaf age.
d): (Growth of hybrid rice/mean of parental varieties) × 100.

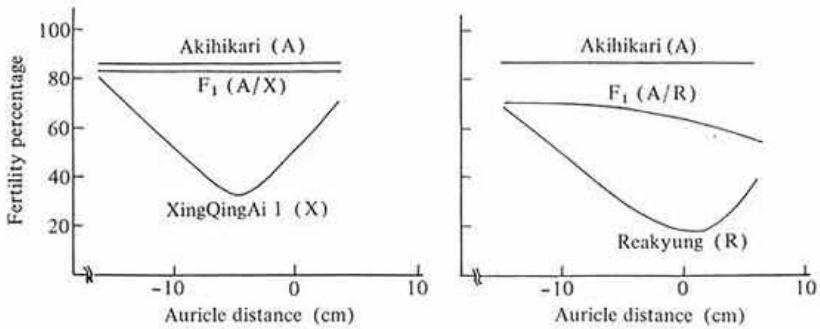

Fig. 5. Effects of low temperature on fertility percentage
Low temperature treatment was conducted at the reduction division stage of pollen for 7 days at 18°C.

efficiency expressed by the relationship between the growth of organs and consumption of endosperm. On the other hand, Blanco et al.[3] reported that the difference in initial growth between Japonica-Indica hybrids and their parental varieties was not significant. Japonica-Indica hybrid rice lines in this experiment behaved like those described by the latter author and growth was not conspicuous until transplanting.

Vigorous tillering mainly accounted for the high degree of heterosis in these lines, through which the highest crop growth rate (CGR) was attained in the initial 30-day period after transplanting. Matsuba et al.[6] reported the appearance of tillers from the 1st node which seldom produces tillers in other varieties. The role of the photosynthetic activity in heterosis of hybrid rice has been examined by many researchers and both positive[7] and negative[5,15] results have been reported. Leaf photosynthesis per unit area did not differ significantly between the hybrid rice lines and the parental varieties in this experiment. These results suggest that the expansion of leaf area due to the increased number of tillers was the main factor for achieving heterosis in the growth of hybrid rice.

The rate of increase in the tiller number slowed down and decreased abruptly 30 days after transplanting until heading. Accordingly, the degree of heterosis in CGR decreased thereafter. This trait of hybrid rice which has been reported by other researchers[4,9,10] may be due to the decrease of NAR with mutual shading of leaves and shortage of nutrients in soil after vigorous growth at the initial stage. Application of fertilizers at this stage was effective in enhancing heterosis in growth in hybrid rice.

Growth after heading was characterized by a high and low CGR in the hybrid rice lines and Indica varieties, respectively. The same tendencies have been reported by other researchers, who indicated that the Japonica-Indica hybrid rice lines exhibited a higher root activity[8] and higher NAR[9] after heading. Dry matter production after heading remarkably affects the ripening of rice. The contribution of dry matter produced after heading to yield was calculated by dividing the total increase in dry weight by the increase in dry weight in the panicles. The value was higher in the hybrid rice lines and Japonica varieties than in Indica varieties. It has been stated that one of the characteristics of high-yielding Indica varieties is the large capacity to translocate non-structural carbohydrates from the culm even if the amount of dry matter production is low in these varieties. Xiang et al.[12-14] reported that although dry matter production in the Chinese Indica-Indica hybrid rice lines in the ripening period was low, the amount translocated from shoots was twice as large as that in ordinary varieties. These hybrid rice lines resembled the Indica varieties in which the contribution of dry matter production to the increase of panicle weight was low. The Japonica-Indica hybrid rice lines used in this experiment resembled the Japonica varieties in the pattern of ripening. However their dry weight was large due to heterosis in growth before heading which can be used as a source of translocation. The large amounts of fertilizer applied induced the increase in dry matter production in hybrid rice. Thus, the Japonica-Indica hybrid rice lines were able to achieve a high yield in terms of dry matter production.

Agata[1] reported that the high yield of Chinese Indica-Indica hybrid rice lines could be mainly ascribed to the large number of spikelets and relatively high percentage of ripening. The large number of spikelets was associated with large panicles. The number of panicles was smaller than that of the parental varieties. The hybrid rice lines in this experiment were obtained by crossing Japonica varieties with the panicle number type and Indica varieties with the panicle weight type, which resulted in hybrid rice lines intermediate between both varieties. The 1000 grain weight was higher than that of the parental varieties though the percentage of ripening was somewhat lower than that of the parental varieties due to hybrid sterility. Thus, the high yield of the hybrid rice lines was derived from complex factors relating to yield components, i.e. a product of additive effects. As for the relationship with dry matter production, hybrid rice displays an efficient sink formation in terms of unit dry matter production as well as a high potential of ripening due to the vigorous dry matter production after heading. Appropriate application of fertilizer was both effective in enhancing the dry matter production and increasing the yield.

Tolerance to unfavorable environments, especially to low temperature is critical to rice cultivation in northern Japan. Indica varieties tend to be so

weak that they cannot be utilized in these areas even if their yield potential is high. Tajima et al.[11] performed a genetic analysis of tolerance to chilling injury in rice seedlings by hybridizing Japonica and Indica varieties. Tolerance of the F_1 was the same as that of the tolerant Japonica varieties and F_2 segregated to 3:1, tolerant and intolerant, respectively. These results indicated that the tolerance to chilling injury was controlled by a single dominant gene. The growth at a low temperature in this experiment also showed a similar tendency, which implies that the hybrid rice lines were able to overcome the weakness of Indica varieties in growth at the vegetative stage. Tolerance to low temperature damage at the pollen reduction division stage was intermediate between that of Japonica and Indica varieties in hybrid rice. Shading treatment at the heading stage caused a high percentage of sterility in hybrid rice, presumably due to the inhibition of fertilization associated with the low viability of pollen. Thus, while hybrid rice lines are superior to Indica varieties in the growth at the reproductive stage, they require further improvement for adjustment to the environment in northern Japan.

In conclusion, Japonica-Indica hybrid rice lines gave a high yield due to the high potential of sink formation accompanied by vigorous dry matter production. They also displayed a higher tolerance to unfavorable environments and appeared to be a promising material for superhigh yield trials in northern Japan through the improvement of the remaining defects.

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