Yields of an F₁ Hybrid and its Parental Rice Cultivars under Different Environmental Conditions

Masayuki MURAI¹⁾, Fujio TOMIKAWA²⁾, Hidehiko TANAKA³⁾, Akihito KUSUTANI⁴⁾
and Shigeyuki SENDO²⁾

¹⁾ *College of Agriculture and Veterinary Medicine, Nihon University, Setagaya-ku, Tokyo 154*

²⁾ *Hokkaido Prefectural Plant Genetic Resources Center, Takikawa 073*

³⁾ *Rice Crop Division, Hokkaido Central Agricultural Experiment Station, Iwamizawa 069-03*

⁴⁾ *Faculty of Agriculture, Kagawa University, Miki-cho 761-09*

One of the F₁ hybrids, which showed comparatively high yield (MURAI and KINOSHITA 1986), and its parental cultivars were grown under 8 environments involving different locations, fertilizer levels and planting densities. The F₁ showed the highest yield of the three genotypes at most of the environments. Fertilizer level was a predominant environmental factor affecting yield. The regression coefficients by FINLAY and WILKINSON (1963) for the three genotypes were around 1.0. These regression coefficients were not significantly different with each other, indicating similar responses among the F₁ and parents. The percentage of ripened grains of the F₁ was the highest of the three genotypes, contributing to the heterosis in yield. Similar extent of heterosis was recognized in harvest index. In dry weight at heading, however, the value of the F₁ was smaller than that of mid-parent at the most of the environments. Therefore, it is concluded that the high yield of the F₁ depended on high dry matter production after heading and smooth grain filling.

KEY WORDS: *oryza sativa* L, Rice, heterosis, genotype-environment interaction, fertilizer, planting density, harvest index.

Introduction

There have been many studies about heterosis in rice from the first report of JONES (1926). Heterosis over higher-parent in yield was recognized for F₁'s between indica varieties (VIRMANI *et al.* 1982, SAINI *et al.* 1974, etc.), for F₁'s between japonica varieties (MURAYAMA 1972ab, 1973 and 1974, KAWASE and HARADA 1982, and MURAI and KINOSHITA 1986), and for F₁'s between japonica varieties and indica varieties (JENNINGS 1966, and MARUYAMA 1990). In the People's Republic of China, F₁ cultivars by the exploitation of the cytoplasmic male sterility are cultivated for one third or more of the total rice area (KOGA 1987 and ARAKI 1990). F₁ cultivars of the Japonica type and those of the Indica type distributed in the north and south of China, respectively, divided by Chang Jiang (the Yangtze River) (KOGA 1987). F₁'s between the japonica and the indica have disadvantages of high amylose content, shattering and sensitiveness to cool temperature, even if the problem of hybrid sterility is solved (MARUYAMA 1989). Hence, it is easier to employ F₁'s between japonica varieties for the practical use in Japan, provided that they exhibit sufficient heterosis.

In this study, one of the F₁ hybrids, which showed comparatively high yields in the

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previous paper (MURAI and KINOSHITA 1986), and its parental japonica cultivars were grown under 8 environments involving different locations, fertilizer levels and planting densities. FINLAY and WILKINSON (1963) devised a measure of adaptability: the regression coefficient of yields of each variety on the mean yield of all varieties at each environment. This measure is adopted to estimate extent of response of each genotype in this study. Further, the F_1 and parents are compared in yield components and harvest index under each environment, and the cause of high yield of the F_1 is inferred.

Materials and Methods

One of the F_1 hybrids, which exhibited comparatively high yields (MURAI and KINOSHITA 1986), was used. The female and male parents, Ishikari and Shiokari were developed in the Hokkaido Prefectural Kamikawa Agricultural Experiment Station (SHIBATA 1980). The parents of Ishikari were Yukara and Sasahonami. The parents of Shiokari were the F_1 of Megurosakaemochi $\times$ Kyowa, and Kyowa. Shiokari is of intermediate culm length, and was one of the leading varieties in Hokkaido around 1970 (EBE 1982). Ishikari is a short culm and high-yielding cultivar, and was cultivated for 32~41% of the total rice area of Hokkaido from 1975 to 1981. The female parent was pollinated with the male parent after castration with a pincette in this study.

Table 1 shows the location, year, method of cultivation, and heading dates in the experiments. The experiments were conducted at three locations: the Hokkaido Prefectural Kamikawa Agricultural Experiment Station in Asahikawa, the Rice Crop Division of the Hokkaido Central Agricultural Experiment Station in Iwamisawa, and the Hokkaido Prefectural Plant Genetic Resources Center in Takikawa. Three fertilizer levels and two planting densities (seedling number per hill) were set at the Resources Center. Two replicates were set at each

Table 1. Cultivation methods and heading dates

Location	Year	Fertilizer ⁴⁾ N-P ₂ O ₅ -K ₂ O (kg/10a)	Seedling number per hill	Planting distance (cm $\times$ cm)	Date of		Heading date		
					Sowing	Trans- planting	F_1	Ishikari	Shiokari
Kamikawa ¹⁾	1987	12.0-9.0-8.0	2	30.0 $\times$ 13.3	Apr. 18	May 23	July 25	July 25	Aug. 2
Central ²⁾	1988	8.0-9.8-6.9	1	30.0 $\times$ 16.7	Apr. 26	May 24	Aug. 10	Aug. 10	Aug. 12
Resources Center ³⁾	1989	9.0-9.0-9.0	2	36.0 $\times$ 12.0	Apr. 22	May 26	Aug. 4	Aug. 4	Aug. 5
"	"	"	1	"	"	"	Aug. 4	Aug. 5	Aug. 6
"	"	6.0-6.0-6.0	2	"	"	"	Aug. 2	Aug. 3	Aug. 3
"	"	"	1	"	"	"	Aug. 4	Aug. 4	Aug. 4
"	"	0.0-0.0-0.0	2	"	"	"	Aug. 4	Aug. 4	Aug. 4
"	"	"	1	"	"	"	Aug. 1	July 30	Aug. 1

¹⁾ Hokkaido Prefectural Kamikawa Agricultural Experiment Station.

²⁾ Rice Crop Division, Hokkaido Central Agricultural Experiment Station.

³⁾ Hokkaido Prefectural Plant Genetic Resources Center.

⁴⁾ All of the fertilizers were applied by basal dressing.

environment. Fifty hills per plot were cut at the ground level at maturity, and total weight and yield of brown rice were measured after air-drying. Ten hills per plot were sampled at heading to measure the total dry weight except the roots. The percentage of ripened grains was investigated by the use of salt solution at the specific gravity of 1.06 (MATSUSHIMA 1957).

FINLAY and WILKINSON (1963) attempted to interpret varietal adaptability by the use of two indices: 1) the regression coefficient of yields of each variety on the mean yield of all varieties at each environment (b-FW), and 2) the mean yield of each variety over all environments. A value of b-FW smaller than 1.0 indicates high stability (= low response), while that larger than 1.0 indicates low stability (= high response). MATSUO *et al.* (1972) reported a significant difference of b-FW in rice varieties. This method was applied to data of this study, although the number of genotypes tested was only three. The procedure of analysis of variance concerning this method followed the report of OKUNO *et al.* (1971).

Results

Fig. 1 shows brown rice yields of the F₁ hybrid and its parental cultivars at each environment. The F₁ shows the highest yield of the three genotypes at all the environments except the Kamikawa Station. At this station, lodging was observed for about 50% of the hills of the F₁ at maturity resulting in some decrease in yield, but the parents showed no lodging. The yield of Ishikari was higher than that of Shiokari at 5 of all the 8 environments. At the Kamikawa Station, the yield of Shiokari was about 200 kg/10a lower than the other two genotypes, because Shiokari showed a higher percentage of sterile spikelets measured by touching fingers than the other two genotypes (those of Shiokari, Ishikari and the F₁ were 33.7, 16.2 and 20.7%, respectively). At this station in this year, cloudy or rainy days continued from July 30 to Aug. 6, during which daily mean temperatures were lower than 19°C. Ishikari and the F₁ headed on the same day, July 25, and Shiokari headed on Aug. 2 (Table 1). Hence, Shiokari suffered the cool temperature damage at flowering, while Ishikari and the F₁ almost completed flowering before the cool duration.

The regression analysis of FINLAY and WILKINSON (1963) was conducted for data of 5 environments, excluding data of the Kamikawa Station, and those of the two environments of no fertilizer application at the Resources Center in which unusually low yields were shown (Fig. 1). Table 2 shows the regression coefficient of each genotype and its mean yield over the 5 environments. The regression coefficients of the three genotypes for the 5 environments were around 1.0, and were highly significant. Table 3 indicates that the regression coefficients were not significantly different with each other. Therefore, it seems that the difference of the responses of the three genotypes was small. When calculated for data of 7 environments including the two environments of no fertilizer application, significant regression coefficients around 1.0 for the three genotypes were obtained (those of the F₁, Ishikari and Shiokari were 1.081, 0.946 and 0.973, respectively). Table 4 shows analysis of variance at the Resources Center, indicating a large effect of fertilizer and a significant effect of seedling number per hill. Further, the highest yields of all the data of all the genotypes over all the environments were those of Ishikari and the F₁ at the Kamikawa Station in which the

Mean yield of the F_1 and parents at each environment
(kg/10a) (x)

Fig. 1. Yields of the F_1 hybrid and its parental cultivars at each environment.

¹⁾ N kg/10a and [seedlings/hill] at the Resources Center.

Δ F_1 . $\circ$ Ishikari. $\times$ Shiokari.

The regression lines by FINLAY and WILKINSON (1963), using data of 5 environments with the exception of data of the Kamikawa Station and those of the two environments of no fertilizer application at the Resources Center:

— $y = 1.114x - 19.026$; F_1 .

- - - $y = 0.829x + 70.787$; Ishikari.

. . . $y = 1.072x - 59.263$; Shiokari.

Table 2. The regression coefficient of each genotype and its mean yield over 5 environments, excluding data of the Kamikawa Station and those of the two environments of no fertilizer application at the Resources Center

	F_1	Ishikari	Shiokari
Regression coefficient ¹⁾	1.114**	0.829**	1.072**
Mean yield over 5 environments (kg/10a)	537	485	476

** Significant at the 0.01 level.

¹⁾ The regression coefficient of yields of each genotype on the mean yield of all genotypes at each environment.

Table 3. Analysis of variance for yield, containing the component of the regression by FINLAY and WILKINSON (1963)

Source of variation	d.f.	F
Genotypes	2	12.91**
Environments ¹⁾	4	20.64**
Interaction	8	0.76
{ Regressions ²⁾	2	0.01
{ Residuals	6	1.02
Block	5	2.68
Error ³⁾	10	

** Significant at the 0.01 level.

¹⁾ Five environments with the exception of the Kamikawa Station and the two environments of no fertilizer application at the Resources Center.²⁾ Difference of regression among genotypes.³⁾ The mean square of error is 850.15.

Table 4. Analysis of variance for yield at the Resources Center (Three-factor experiment)

Source of variation	d.f.	F
Genotypes (G)	2	6.07*
Fertilizer levels (F)	2	334.34**
Seedlings/hill (S)	1	19.55**
G × F	4	0.52
G × S	2	0.70
F × S	2	0.55
G × F × S	4	0.31
Block	6	1.58
Error ¹⁾	12	

*, ** Significant at the 0.05 and 0.01 levels, respectively.

¹⁾ The mean square of error is 1152.71.

largest amount of fertilizer of all the environments was applied (Table 1 and Fig. 1). Therefore, it is judged that fertilizer level was the most important factor affecting yield in this study.

Table 5 shows yield components and some other characters at all the environments (numbers in parentheses indicate the percentage of the F₁ to mid-parent value). The percentage of yield of the F₁ to that of mid-parent ranged from 107 to 116% throughout all the environments, and the percentage of the F₁ to that of higher-parent at each environment ranged from 98% (the Kamikawa Station) to 114% (the Central Station) as shown in brackets. The panicle number / m² of the F₁ was the most of the three genotypes at 6 of all the 8 environments. Similarly, the percentage of ripened grains of the F₁ was the highest of the three genotypes at most of the environments. The 1000-kernel weight of the F₁ was heavier than or equivalent to that of mid-parent at all the environments, although it was lighter than that of Ishikari (higher-parent). On the other hand, the F₁ had smaller number of spikelets/panicle than mid-parent at most of the environments.

The harvest index of the F₁ was close to or higher than that of Ishikari (higher-parent) at all the environments except the Kamikawa Station in which lodging was observed for the F₁ (Table 5). The total weight of the F₁ was heaviest of those of the three genotypes at 5 of all the 8 environments. In dry weight at heading, however, the value of the F₁ was smaller than that of mid-parent at 4 of the 7 environments in which this character was measured. The LAI of the F₁ was close to that of the lower-parent, Ishikari (data only at the Kamikawa Station).

Discussion

There are a few reports on response of F₁ hybrids to environmental factors. VIRMANI *et al.* (1982) reported that most of the F₁'s used specifically adapted to either wet season or

Table 5. Yield components and some other characters, and the percentage of the F₁ to mid-parent value in parentheses

(1) The Kamikawa Station and the Central Station

Character	Kamikawa			Central			LSD _(5%) ³⁾
	F ₁	Ishikari	Shiokari	F ₁	Ishikari	Shiokari	
Yield of brown rice (kg/10a)	673 (115) [98]	687	482	613 (116) [114]	522	540	65
Panicles/m ²	747 (103)	781	663	539 (129)	427	409	71
Spikelets/panicle ¹⁾	59.2 (95)	55.4	69.7	—	—	—	12.1
Percentage of ripened grains	71.3 (110)	70.7	58.9	—	—	—	14.0
1000-kernel weight (g)	21.4 (106)	22.5	17.7	—	—	—	0.5
Harvest index (%)	44.8 (111)	47.8	33.3	46.8 (103)	47.2	44.0	4.6
Total weight (kg/10a)	1475 (104)	1415	1419	1310 (112)	1105	1228	118
Dry weight at heading (g/m ²)	730 (94)	711	836	—	—	—	60
LAI at heading	4.3 (90)	4.4	5.3	—	—	—	1.3
Culm length ²⁾ (cm)	—	—	—	62.8 (103)	57.2	65.1	4.6

(2) 9N/10a at the Resources Center

Character	2 seedlings/hill			1 seedling/hill		
	F ₁	Ishikari	Shiokari	F ₁	Ishikari	Shiokari
Yield of brown rice (kg/10a)	579 (111) [108]	535	510	529 (112) [109]	485	459
Panicles/m ²	492 (111)	432	455	433 (110)	361	430
Spikelets/panicle ¹⁾	60.2 (90)	63.5	70.3	63.9 (98)	69.4	61.2
Percentage of ripened grains	84.6 (110)	76.5	77.9	82.3 (104)	74.8	83.9
1000-kernel weight (g)	23.1 (100)	25.5	20.5	23.3 (100)	25.9	20.8
Harvest index (%)	49.0 (105)	50.2	42.9	49.2 (105)	49.0	45.2
Total weight (kg/10a)	1170 (105)	1051	1172	1064 (108)	978	1001
Dry weight at heading (g/m ²)	463 (95)	438	536	435 (89)	485	491
Culm length ²⁾ (cm)	68.5 (102)	60.0	74.3	68.9 (105)	59.6	72.3

dry season in Philippines. DAVIS and RUTGER (1976) reported that four F₁ hybrids exhibited no heterosis over higher-parent in yield when cultivated by a dense planting (15 × 15 cm). MURAYAMA (1973) recognized that some F₁'s exhibited heterosis in yield constantly under four cultural conditions combining high and standard fertilizer levels, and narrow and standard planting distances. In this study, the heterosis over higher-parent was shown at most of the environments. It is inferred that the comparatively small extent of heterosis of the F₁ is due to the high yield abilities of the parents. The regression analysis indicates similar responses among the F₁ and the parents. Fertilizer level was a predominant environmental factor affecting yield in this study.

(3) 6N/10a at the Resources Center

Character	2 seedlings/hill			1 seedlings/hill		
	F ₁	Ishikari	Shiokari	F ₁	Ishikari	Shiokari
Yield of brown rice (kg/10a)	506 (107) [104]	461	488	458 (112) [109]	421	383
Panicles/m ²	384 (116)	316	345	336 (104)	319	327
Spikelets/panicle ¹⁾	60.6 (84)	62.8	81.6	62.8 (104)	57.0	64.2
Percentage of ripened grains	89.8 (105)	89.4	81.8	89.0 (103)	88.4	85.2
1000-kernel weight (g)	24.2 (103)	26.0	21.2	24.4 (102)	26.2	21.4
Harvest index (%)	51.7 (103)	51.5	48.5	51.2 (103)	51.5	48.1
Total weight (kg/10a)	964 (103)	885	994	884 (111)	803	784
Dry weight at heading (g/m ²)	368 (100)	350	385	290 (95)	286	327
Culm length ²⁾ (cm)	64.3 (103)	55.9	68.8	63.8 (104)	56.6	65.9

(4) ON/10a at the Resources Center

Character	2 seedlings/hill			1 seedlings/hill		
	F ₁	Ishikari	Shiokari	F ₁	Ishikari	Shiokari
Yield of brown rice (kg/10a)	213 (113) [112]	187	190	171 (109) [101]	169	144
Panicles/m ²	243 (104)	240	230	183 (100)	195	173
Spikelets/panicle ¹⁾	41.8 (97)	40.7	45.9	43.6 (94)	42.9	49.5
Percentage of ripened grains	84.8 (107)	74.7	83.8	89.0 (112)	79.2	79.6
1000-kernel weight (g)	24.7 (105)	25.7	21.5	24.1 (103)	25.6	21.1
Harvest index (%)	46.4 (113)	43.9	39.5	46.0 (108)	42.8	42.5
Total weight (kg/10a)	450 (101)	419	474	367 (101)	390	333
Dry weight at heading (g/m ²)	148 (113)	127	135	104 (110)	90	100
Culm length ²⁾ (cm)	49.4 (103)	42.4	53.2	49.3 (101)	44.4	52.9

[]: the percentage of yield of the F₁ to that of higher-parent at each environment.

¹⁾ Estimated by the formula of yield ÷ one kernel weight ÷ ripened grain (%) × 100 ÷ panicles/m².

²⁾ Longest culm in each hill.

³⁾ From analysis of variance using all the data at all the environments in which each character was measured.

There are few reports on heterosis for the percentage of ripened grains, in which insufficiently ripened grains were distinguished by any method. In this study, the percentage of ripened grains of the F₁ was the highest of the three genotypes, contributing to the heterosis in yield. Similar extent of heterosis was recognized in harvest index. In dry weight at heading, however, the value of the F₁ was smaller than that of mid-parent at the most of the environments. Therefore, it is concluded that the high yield of the F₁ in this study depended on high dry matter production after heading and smooth grain filling.

At the highest fertilizer level of the Kamikawa Station, lodging was shown for about 50% of the hills of the F₁, although the parents showed no lodging. The culm length of the F₁

was longer than that of mid-parent at all the environments in which this character was measured (Table 5). Studies by diallel analysis indicate positive dominance in culm length (LI and CHANG 1970, MURAYAMA 1972a, and MURAI and KINOSHITA 1986). Therefore, a following suggestion may be advanced: when an F_1 -cultivar adaptable to high fertilizer level is developed, its parents had better possess an identical dwarfing gene e.g. *d-47(t)* (dee-geo-woo-gen dwarf) or other genes enhancing stiffness of culm. A similar suggestion was given by MARUYAMA (1989). On the other hand, the yield of the F_1 was 14% higher than that of Ishikari at the environment of no fertilizer and two seedlings per hill (calculated from Table 5-(4)). This supports that there is a possibility that an F_1 cultivar adaptable to low fertilizer level can be developed. However, this study is the results of only one hybrid. Further studies are needed to clarify the adaptability of F_1 hybrids in rice.

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水稻の F_1 とその両親品種の異なる環境条件下における収量村井正之¹⁾・富川富士夫²⁾・田中英彦³⁾楠谷彰人⁴⁾・千藤茂行²⁾¹⁾日本大学農獣医学部, 東京都世田谷区 〒154²⁾北海道立植物遺伝資源センター, 滝川市 〒073³⁾北海道立中央農業試験場稲作部, 岩見沢市 〒069-03⁴⁾香川大学農学部, 三木町 〒761-09)

前報 (MURAI and KINOSHITA 1986) において, 北海道品種間の F_1 の幾つかにヘテロシスが認められたことを報告した。本報では, それらのうちの1つであるイシカリ×しおかりの F_1 および両親を, 場所, 年次, 肥料水準ならびに栽植密度の異なる8種の環境条件のもとに栽培し, F_1 の環境反応を解析した。実験は, 北海道立上川農業試験場, 同中央農業試験場稲作部ならびに同植物遺伝資源センターにて行った (Table 1)。植物遺伝資源センターでは, 3水準の肥料条件ならびに1本植と2本植の栽植密度を設定した。また, 収量構成要素や収穫指数等を調べることによって F_1 の多収の原因を検討した。

上川農試を除く他の7環境のすべてにおいて, F_1 の収量 (精玄米重) は最も高かった (Fig. 1)。上川農試では, F_1 の成熟期に約50%の倒伏がみられ, それが収量を低下させたと推定される (両親には倒伏がみられなかった)。8環境中の5環境において, イシカリの収量はしおかりより高かった。なお, 上川農試において, しおかりが F_1 やイシカリより約200 kg/10a 低収量であったのは, その開花期が低温であったための不稔が生じたことに起因する。

上川農試および他より著しく低収量の植物遺伝資源センターの無施肥の2環境を除く5環境に対して, FINLAY and WILKINSON (1963) の回帰分析が行われた (Fig. 1)。 F_1 と両親の回帰係数は, 1.0 前後であり, いずれも有意であった (Table 2)。しかし, F_1 と両親の相互間には有意差がみられなかった (Table 3)。したがって, F_1 と両親のこれらの環境に対する反応の差異は小さいと推定された。Table 4は, 植物遺伝資源センターにおける収量の分散分析であり, 肥料水準の著しく大きな効果を示しており, 栽植本数の効果も有意であった。また, すべての環境を通じて最も多収であったのは, 上川農試のイシカリと F_1 であり, その上川農試における施肥量は全環境で最も多かった。したがって, 肥料水準は最も効果の大きい環境要因であったといえる。

Table 5は, 各環境における収量およびその関連形質である。 F_1 の収量は, 中間親に対して107~116%であった。また, 各環境の高収の方の親に対しては, 98% (上川農試) ~114% (中央農試) であった。穂数/m²では, 8環境中の6環境において, F_1 が両親より多かった。登熟歩合でも, 7環境 (中央農試未調査) のうちの6環境において F_1 が両親より高かった。玄米千粒重においては, F_1 の値は, 中間親以上であったがイシカリ (大きい方の親) より小さかった。しかし, 1穂類花数では, F_1 は中間親より少なかった。収穫指数では, 上川農試を除いて, F_1 はイシカリ (高い方の親) と同程度もしくはそれ以上の値を示した。しかし, 出穂期乾物重では, 調査した7環境のうちの無肥の2環境を除く5環境において, F_1 は中間親以下の値を示した。これらより, F_1 の多収は, 出穂後の物質生産量が多く且つ登熟が良好であることに起因したといえる。

F_1 は, いずれの環境でも中間親より長稈であり (Table 5), 上川農試の多肥条件では倒伏がみられた。したがって, 多肥条件で多収な F_1 を育成するときには, 耐倒伏性に留意する必要があると考えられる。 F_1 は, 無肥条件において両親より多収であった (Table 5-(4))。これは, 少肥向けの F_1 品種を育成できる可能性があることを示唆している。