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SCREENING AND GENETIC ANALYSIS OF WIDE-COMPATIBILITY IN F_1 HYBRIDS OF DISTANT CROSSES IN RICE, ORYZA SATIVA L.

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INTRODUCTION

The sterility problem in the wide crosses of rice is unique. In most cases, seed for F_1 hybrids can be easily obtained, but partial sterility is commonly found in the F_1 of distant crosses. The semi-sterile plants are also reproduced through early generations. Although the degree and the frequency of the partial sterility are overwhelming, rice breeding by means of wide crosses has been attempted, and was successful in some cases (Ghose *et al,* 1960; Parthasarathy, 1972; Balakrishna Rao, 1978). In Korea, extensive trials of Indica-Japonica crosses were successful through backcrossing of Indica high yielding varieties into Indica-Japonica crosses (Chung and Heu, 1981).

The partial sterility in early generations can be attributed to the heterozygous status. F_1 weakness is also known as a barrier to wide crosses (Sato and Hayashi, 1983). Another type of partial sterility is also frequent in homozygous lines (Kitamura, 1962, 1963; Oka and Doida, 1962; Yokoo, 1984). The relative importance of these reproductive barriers between different groups of rice can not be easily evaluated, as there are few surveys. The sterility problem is not an absolute barrier to wide-cross breeding in rice, but if there were any means to solve the problem, rice breeding would become more successful.

Past studies on cultivated rices showed that some varieties give good F_1 fertility in their crosses to Indica as well as to Japonica varieties (Terao and Mizushima, 1939; Morinaga and Kuriyama, 1958; Heu, 1967). In a review of these works, Ikehashi (1982) emphasized the need for systematic screening and utilization of such wide-compatibility varieties (WCVs) to overcome the reproductive barrier. If the genic mechanism for the wide-compatibility is simple, it could be applied to the system of hybrid seed production, or be used for breeding Indica-Japonica hybrids.

In the present study, firstly a series of varietal screenings was attempted to identify the wide-compatibility types. And, after finding such varieties, the genetic mechanism for the wide-compatibility and the partial sterility was analyzed through the evaluation of two contrasting models proposed by Oka (1953) and Kitamura (1962). As a result, an allelic interaction at a locus was found to be the basis for the F_1 sterility. Based on this finding, the extent to which the wide-compatibility gene is effective was studied with different varietal groups, and the effect of the allelic interaction on the sterility in the early generations was also studied.

The method for minimizing the number of genotypes by backcrossing, while analyzing the relation between marker genotypes and the level of semi-sterility, was extremely useful in determining the genetic mechanism of the sterility.

The results of the present studies led the authors to a critical review of previous works. Some controversial points will be discussed in the respective chapters. The understanding of the genetic mechanism of sterility and wide-compatibility is expected to facilitate wide cross breeding in rice.

The term 'compatibility' will imply hereafter a measure of similarity given by the fertility of F_1 hybrids between two varieties. Due to the ambiguity of the definition, the terms of Indica and Japonica were not written in italic letters in the present paper.

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I. Analyses of F_1 fertility of hybrids between different groups of cultivated rices

To identify the wide-compatibility type, a total of 80 varieties, most of which are Aus or Javanica varieties, was crossed to an Indica and a Japonica tester variety, and the pollen and spikelet fertility of the resultant F_1 hybrids was examined.

The results of the initial tests until 1983 were published in 1984 (Ikehashi and Araki), however, a large number of related crosses have been tested in each varietal group since then. Accordingly, the initial data and additional ones will be listed together for each of the varietal groups.

Except for the initial tests at Tsukuba, all the data were obtained at the Okinawa Branch of the Tropical Agriculture Research Center on Ishigaki island in Okinawa prefecture. Under the subtropical climate, rice plants were cultivated twice a year, and little affected by cold temperature which is a major factor of interfere with the level of pollen or spikelet fertility.

Materials and Methods

For a systematic screening of wide compatibility, it is necessary to choose appropriate standard varieties as testers for hybridization. Except for a preliminary test, IR 36 and IR 50 were used as Indica testers representing widely cultivated Indica varieties. Nihonmasari and Akihikari were used as Japonica testers which represent leading varieties in Japan. A breeding line, Tohoku 127 was used as a substitute for Akihikari when Akihikari was not available. Tohoku 127 is a progeny from an Akihikari cross.

In 1979, from the collection of the National Institute of Agricultural Sciences (NIAS) six varieties including Aus and Indonesian varieties were chosen and crossed to each of the Indica and Japonica testers. Ten panicles each collected from a single F_1 plant were examined to determine the spikelet fertility. The spikelet fertility was determined by counting the number of fertile and empty spikelets in each panicle.

From 1980 to 1983, 24 Indonesian native varieties of the tall upland type (Javanica varieties) were crossed to an Indica (IR 36 or IR 50) and to a Japonica variety (Akihikari or Tohoku 127). In the same period, 25 varieties from the Aus group were crossed to the testers. In 1984, a set of 14 Aus varieties was added to the compatibility test. Also, 16 varieties which were found to be tolerant of salinity, drought or peat soil were tested by the same method. Such stress-tolerant varieties can be primarily used in distant crosses. All the varieties were provided by NIAS, the International Rice Research Institute (IRRI), or Central Agricultural Experiment Station (CAES). In the last part of the compatibility tests, some Bhutan varieties provided by Hokkaido Nat. Agr. Exp. Stn. were added to the tests.

From the initial tests, it was possible to classify several compatibility types in the Javanica as well as in the Aus varieties. Accordingly, additional crosses were made between different types within each varietal group and the resultant F_1 hybrids were tested for their fertility from 1983 to 1985. Additional crosses between Javanica and Aus varieties were also tested in the same period.

For all the crosses, pollen and spikelet fertility of the F_1 hybrids was determined as the indicator of the compatibility. In the determination of the pollen fertility one or two panicles were taken just before flowering for laboratory examination. Anthers were collected from several opening spikelets on a glass slide on which a drop of acetocarmine was placed. After dispersing pollen from anther by pressing the cover glass, the number of fertile and abortive pollen grains were counted with a microscope at a magnifying power of 200 times. For each sample the inspection was repeated ten times to scan a total of about 300 grains. The spikelet fertility was occasionally affected by pests, especially by bug, cool wind, and so on. It was particularly so in 1981, so that the maximum spikelet fertility of ten samples was listed for each of the F_1 hybrids. In the later tests two or three visually good panicles were chosen to give a mean spikelet fertility.

In the compatibility tests, the degree of pollen fertility is found to be independent of spikelet sterility. Therefore, each variety was routinely examined for four independent fertility determinations, namely, the pollen and the spikelet fertility in each cross to an Indica and Japonica tester.

Table 1-1. Spikelet fertility of wide-compatibility varieties and their F_1s with Indica or Japonica testers at NIAS in 1980

Varieties or F_1s	Date of heading	Spikelet fertility %	
		Mean	Range
Calotoc	Aug. 27	78.7	96 - 60
Nihonmasari/Calotoc	Sep. 1	94.0	99 - 89
IR 36/Calotoc	Aug. 26	82.3	95 - 71
Ketan Nangka	Aug. 20	86.7	94 - 71
Nihonmasari/Ketan Nangka	Sep. 13	96.2	98 - 94
IR 36/Ketan Nangka	Aug. 19	80.2	86 - 76
- ditto -	Aug. 30*	91.2	95 - 85
- control -			
Nihonmasari	Aug. 14	96.2	100 - 90
IR 36	Aug. 20	77.7	84 - 71
Nihonmasari/IR 36	Aug. 30	64.1	73 - 57
IR 36/Nihonmasari	Sep. 4	67.9	76 - 64

The data marked with * were derived from late planted plots.

Results

1. Wide-compatibility varieties (WCV)

The results of the analysis of the spikelet fertility of the WCV and their F_1 are listed in Table 1-1 along with those on the spikelet fertility of the F_1s between the testers. The spikelet fertility of parent varieties, which indicates the level of fertility for a compatible F_1, ranged from the highest value of 96.2 percent in Nihonmasari to the lowest of 77.7 in IR 36, and was more than about 90 percent maximum for each variety except IR 36. The fertility of F_1 hybrids between the Indica and the Japonica tester ranged from 64.1 to 67.9 percent. Therefore, when the maximum spikelet fertility in a F_1 hybrid was close to 90 percent, the F_1 was rated as fertile as a variety. On the other hand, when the F_1 fertility did not exceed the level of 75 percent, such a cross was considered to be partially sterile.

Table 1-2. Pollen fertility of F_1 hybrids between WCVs and Japonica or Indica testers

Crosses	Year	No. of plants	Mean fertility %
IR 36/Calotoc	1981	16	98.2
IR 36/Calotoc	1982	23	99.3
Calotoc/IR 36	1982	12	99.3
Mihonmasari/Calotoc	1982	18	99.4
Calotoc/Nihonmasari	1982	4	98.8
IR 36/Ketan Nangka	1981	11	97.2
IR 36/Ketan Nangka	1982	19	93.2
Kochihibiki/Ketan Nangka	1982	10	93.9
IR 36 - Control	1982	15	99.0

Table 1-3. Pollen fertility of F_1 hybrids between Japonica and Indica testers

Crosses (Year)	No. of plants in fertility class						Total	Mean
	-50	-60	-70	-80	-90	-100 %		fertility %
Nihonmasari/IR36 (1981)		1	6	15	7		29	75.3
Nihonmasari/IR36 (1982)	3	6	2				11	56.6
IR36/Nihonmasari (1982)		5	6	2			13	61.6

Table 1-4. Wide compatibility of CPSLO 17 and Ketan Nangka revealed in F_1 fertility of distant crosses

Varieties or F_1s	Year of the test	Fertility %	
		Pollen	Spikelet
CPSLO 17	1982, I	98.5	86.5
SPSLO 17/IR 50		96.1	74.0
SPSLO 17/Akihikari		98.7	73.6
CPSLO 17	1982, II	98.5	76.7
IR 50/CPSLO 17		97.6	93.8
Akihikari/CPSLO 17A		92.5	79.2
IR 50/Akihikari (control)		45.3	42.8
Ketan Nangka/Nihonmasari	1984, II	90.3	87.3
Ketan Nangka/Akihikari		91.5	90.1
Ketan Nangka/IR 36		55.7	97.0

Based on these criteria, Calotoc and Ketan Nangka were confirmed to be 'compatible' with Indica as well as with Japonica varieties (Table 1-1). Calotoc and Ketan Nangka were also found to give fertile F_1 hybrids with respect to pollen fertility when they were crossed to Indica as well as to Japonica varieties (Table 1-2). When Ketan Nangka or Calotoc was crossed to Indica as well as to Japonica testers, their F_1 hybrids showed an almost normal fertility of more than 90 percent, while the F_1s between Indica and Japonica testers gave a pollen fertility of 60—70 percent (Table 1-3).

Reciprocal crosses between Ketan Nangka and tester varieties were tested in 1984 (Table 1-4). From the results obtained, the F_1 hybrids of the Ketan Nangka/Japonica cross showed a normal fertility, however, the F_1 hybrid of Ketan Nangka/IR 36 gave pollen fertility values as low as 55.7 percent. Whether these data can be reproduced should be reassessed later.

Besides, it was confirmed that CPSLO 17 was widely compatible (Table 1-4).

2. Javanica varieties

Compatibility types. Data on the pollen and spikelet fertility of 24 Indonesian varieties and their F_1s with the Indica or the Japonica tester are listed in Table 1-5. A majority of 15 varieties was classified into one group based on their high pollen fertility both with the Indica and Japonica testers, a normal spikelet fertility with the Japonica tester, and clear semi-sterility with the Indica tester. In other words, these 15 varieties were compatible with the Indica and the Japonica testers with regard to pollen fertility, but not so in terms of the spikelet fertility with the Indica tester. Six varieties showed semi-sterility in all the four scores. Two varieties, Sitabo Tabo and Ingsa Putih seemed to belong to an exceptional group with a good spikelet fertility with Japonicas and good fertility with Indicas. Only one variety, Padi Bujang Pendek exhibited a normal fertility in all the four fertility tests. This variety was also remarkable by its sturdy intermediate plant type. One variety named Hawara-geporeck tested in the preliminary study can be added to this group. Hawara-geporeck showed typical F_1 sterility when crossed to IR 36, but normal fertility when crossed to the Japonica tester. Based on these results, the Javanica varieties can be classified into 5 groups as follows:

A. Normal fertility with testers except spikelet fertility with Indica testers: Banten, Baso, Cicih Baat, Cicih Balanak, Cicih Cepaka, Gamah, Karii Rangga, Loktjan, Padi Aban/gogo, Padi Empat Bulan/gogo, Padi Segutuk, Padi Susu, Para Roon Dawa, Renik Beliti, Saba Enim.
B. Partial sterility both with Indica and Japonica testers: Cicih Buleleng, Penuh Baru II, Sigabe Taon, Silewah, Simanuk, Page Leoh.
C. Normal fertility both with Indica and Japonica testers: Padi Bujang Pendek.
D. Exceptional type: Ingsa Putih, Sitabo Tabo.
E. Japonica type: Hawara-geporeck.

Fertility of F_1 hybrids between two different types within Javanica varieties. In the preceding experiment, six Javanica varieties including Penuh Baru II, Page Leoh, Sigabe Taon and Simanuk were not compatible with the Indica or the Japonica tester. However, it was shown that these four varieties, which will be named hereafter 'Penuh Baru Group', were clearly compatible with Ketan Nangka (Table 1-

Table 1-5. Fertility of pollen and spikelet in F_1s of Indonesian varieties and Indica or Japonica testers (TARC, Okinawa, 1981 - 83)

Variety	Source	Fertility of variety %		F_1-fertility %			
				With a Japonica tester		With an Indica tester	
		Pollen	Spikelet	Pollen	Spikelet	Pollen	Spikelet
Test with Tohoku 127 and IR 36 as Japonica and Indica testers, respectively.							
Sigabe Taon	180043	99.3	89.0 (94)	67.5	63.7 (84)	76.3	35.6 (51)
Para Roon Dawa	180046	97.7	75.3 (89)	98.6	68.8 (82)	93.9	39.2 (56)
Padi Segutuk	180050	98.3	71.7 (90)	91.2	69.1 (78)	96.5	37.7
Padi Susu	180051	97.6	immature	97.0	74.5 (90)	86.0	38.8 (48)
Penu Baru II	180054	99.2	87.7 (97)	75.4	44.0 (67)	71.7	42.8 (56)
Simanuk	180062	99.6	72.0 (97)	82.0	57.2 (88)	70.2	40.7 (47)
Cicih Balanak	180068	99.4	immature	87.1	74.5 (83)	93.3	51.5 (59)
Page Leoh	180085	99.1	57.7 (94)	83.6	65.3 (87)	71.5	41.2 (47)
Loktjan	NIAS VT83	99.3	immature	97.0	82.5 (92)	93.5	36.9 (50)
Test with Akihikari and IR 50 as a Japonica and an Indica tester, respectively, in 1982.							
Padi Empat Bulan/gogo	180048	100	92.6	99.0	92.9	91.1	51.7
Saba Enim	180058	96.6	80.8	95.2	75.8	99.5	45.1
Banten	180066	98.8	immature	90.2	80.9	94.9	45.4
Baso	180108	99.4	87.4	93.5	88.2	98.9	56.0
Test with Akihikari and IR 50 as a Japonica and an Indica tester, respectively, in 1983.							
Baten*	180066	97.5	69.9	97.8	89.2	97.1	47.0
Padi Bujang Pendek	180076	—	92.5	97.6	90.8	96.7	80.0
Gamah	180110	99.3	83.1	99.6	89.2	92.4	42.4
Karii Rangga	180112	96.5	—	98.7	85.0	98.3	49.4
Test with Akihikari and IR 36 as a Japonica and an Indica tester, respectively, in 1983.							
Renik Beliti	180057	92.9	80.5	96.6	81.8	98.7	48.2
Sitabo Tabo	180064	98.8	85.3	78.3	85.0	99.0	57.2
Ingsa Putih	180069	94.0	77.8	79.4	78.4	94.2	59.6
Padi Abang/gogo	180074	97.6	79.1	97.5	81.1	92.5	57.1
Cicih Baat	180117	100	88.1	93.9	75.0	94.6	71.7
Cicih Buleleng	180118	98.3	80.7	55.3	85.1	83.1	63.6
Cicih Cepaka	180119	99.7	90.9	91.9	83.0	95.8	51.8
Silewah	IRCTN	98.0	95.6	82.7	69.5	84.7	50.0
Hawara-geporeck	VT63	(Preliminary Test, 1980)		100	91.3	83.3	47.7

* : This variety was tested also in 1982.

Figures in parentheses indicate maximum spikelet fertility of ten samples. In other cases the spikelet fertility is a mean from two or three visually good panicles.

Table 1-6. Pollen and spikelet fertility in F_1 plants from crosses between 'Penuh Baru' group and testers

Varieties or F_1s	Fertility %				Seed source
	1981		1983		
	Pollen	Spikelet	Pollen	Spikelet	(NIAS)
Penuh Baru II	99.2	87.7	98.0	91.3	180054
IR 36/Penuh Baru II	71.7	42.8	75.4	28.6	
Japonica/Penuh Baru II	75.4	44.0	75.6	30.9	
Ketan Nangka/Penuh Baru II			95.5	94.2	
Page Leoh	99.1	57.7	99.3	—	180085
IR 36/Page Leoh	71.5	41.2	73.0	57.1	
Japonica/Page Leoh	83.6	65.3	70.9	77.6	
Ketan Nangka/Page Leoh			96.9	85.9	
Sigabe Taon	99.6	89.0	98.9	97.2	180043
IR 36/Sigabe Taon	76.3	35.6	75.9	59.6	
Japonica/Sigabe Taon	67.5	63.7	70.7	84.8	
K. Nangka/Sigabe Taon			99.2	91.4	
Simanuk	99.6	72.0	99.6	84.0	180062
IR 36/Simanuk	70.2	40.7	77.7	42.5	
Japonica/Simanuk	82.0	57.2	70.8	84.6	
Ketan Nangka/Simanuk			97.6	79.0	

Note: Japonica varieties used were Tohoku 127 and Akihikari, respectively in 1981 and 1983.

Table 1-7. Pollen and spikelet fertility in F_1 plants between 'Banten' group and 'Penuh Baru' group

Varieties or F_1s	Fertility %	
	Pollen	Spikelet
Banten	100	97.9
Banten/Penuh Baru II	99.2	90.8
Banten/Page Leoh	99.4	96.1
Banten/Sigabe Taon	98.7	97.9
Banten/Simanuk	98.1	98.1
Ketan Nangka/Banten	98.3	97.1
Gamah	99.0	100
Bamah/Penuh Baru II	97.5	93.9
Gamah/Page Leoh	99.3	94.1
Gamah/Sigabe Taon	98.5	94.7
Gamah/Simanuk	98.6	95.5
Ketan Nangka/Gamah	99.0	97.3
Saba Enim	98.5	97.3
Saba Enim/Banten	58.5	97.0
Banten/Saba Enim	83.8	98.7
Gamah/Saba Enim	44.2	91.7
Saba Enim/Penuh Baru II	55.3	78.0
Ketan Nangka/Saba Enim	96.0	96.8
Penuh Baru II	99.4	92.1
Page Leoh	100	91.9
Sigabe Taon	98.1	92.2
Simanuk	95.8	93.4

Note: These data were collected in the second season, 1984.

6). Following the results, the compatibility between the Penuh Baru Group and Banten Group which showed spikelet sterility in the F_1 hybrids with IR 36 but normal fertility with the Japonica tester, were tested further. Three varieties of the Banten Group, i.e. Banten, Gamah and Saba Enim showed good compatibility with Ketan Nangka (Table 1-7). Banten and Gamah showed good compatibility with the four varieties of the Penuh Baru group, however, Saba Enim showed incomplete fertility with the other Javanica varieties. F_1s between the varieties of the Penuh Baru group showed normal fertility (Table 1-8). Based on the results, it can be concluded that the F_1 hybrids between different compatibility types in the Javanica group show generally normal fertility with a few exceptions like Saba Enim.

Table 1-8. F_1 fertility in the crosses within 'Penuh Baru' group

Varieties or F_1s	Fertility %	
	Pollen	Spikelet
Sigabe Taon/Simanuk	97.7	95.6
Sigabe Taon/Penuh Baru II	98.1	94.5
Simanuk/Penuh Baru II	96.4	93.4
Penuh Baru II	97.4	94.5
Sigabe Taon	98.9	97.6
Simanuk	98.5	93.9
Page Leoh	98.9	97.4

3. Varieties tolerant of environmental stress

In this group two varieties, Kinandan Patong and Paedai Kulibungga were not photoperiod-sensitive, and their compatibility was clearly of the Japonica type (Table 1-9). All the other entries to the test were strongly photoperiod-sensitive except a variety Palar, a weakly sensitive one. Among the Javanica varieties, Salumpikit and Pulut Daeng Merakka seemed exceptional due to the medium spikelet sterility with the Japonica tester despite fertility in other tests. Pokkali was unique for its marginal pollen fertility with the Indica tester like other varieties from South India, such as Triveni and Eat Samba. The rest of the ten varieties with strong photoperiod-sensitivity were of the Indica type, although Baelaon and Carreon (Acc. 38703) showed marginal pollen fertility with the Japonica tester (Table 1-9). As a result, these varieties can be classified as follows:

A. Indica type: Baelaon, Bajar Putih, Carreon, Ketan Cere, Kuatik Serai, Maraja, Merak, Kuatik Putih, Palar.
B. Japonica type: Kinandang Patong, Paedai Kulibungga.
C. Other types: Pokkali, Pulut Daeng Merakka, Salumpikit.

Table 1-9. Fertility of pollen and spikelet in F_1s between stress-tolerant varieties and Indica or Japonica testers (TARC, Okinawa, 1982-83)

Variety	Source	Origin	Tolerance for	F_1-fertility %			
				With a Japonica tester		With an Indica tester	
				Pollen	Spikelet	Pollen	Spikelet
Test with Akihikari and IR 36 as a Japonica and an Indica tester, respectively, in 1982-83							
Baelaon	Acc. 4191	Indonesia	peat soil1)	88.2	51.5	98.0	86.5
Maraja	Acc. 4197	Indonesia	〃	18.9	10.4	91.9	92.3
Palmar	Acc. 4208	Indonesia	〃	35.4	42.9	90.5	82.8
Salumpikit	Acc. 5423	Philippines	drought2)	92.2	63.9	99.1	82.8
Carreon	Acc. 5993	Philippines	〃	58.5	34.6	95.2	95.2
Ketan Cere	Acc. 35719	Indonesia	〃	49.3	21.4	90.9	81.3
Carreon	Acc. 38703	Philippines	〃	88.8	56.0	98.2	81.7
Kuatik Serai	Acc. 18035	Indonesia	salinity3)	19.2	53.2	98.9	93.7
Merak	Acc. 25457	Indonesia	〃	75.3	48.4	98.9	95.5
Pokkali	Acc. 26869	India	salinity4)	86.8	56.5	83.8	89.6
Test with Akihikari and IR 50 as a Japonica and an Indica tester, respectively, in 1982-83							
Kuatik Putih	Acc. 18037	Indonesia	salinity4)	31.9	44.8	98.4	91.5
Bajar Putih	Acc. 17187	Indonesia	salinity3)	17.3	45.6	99.1	86.7
Kuatik Serai Rendah	Acc. 24739	Indonesia	〃	—	44.6	96.2	91.0
Pulut Daeng Merakka	Acc. 24788	Indonesia	〃	90.4	63.6	93.7	87.6
Kinandan Patong	Acc. 23364	Philippines	drought2)	97.9	89.1	76.2	73.0
Paedai Kulibungga	Acc. 27207	Indonesia	〃	91.6	99.1	4.8	12.3

Information source:
1) IRRI Annual Report for 1978, p.108.
2) IRRI Annual Report for 1979, p.86-87.
3) IRRI Annual Report for 1978, p.108.
4) IRRI Annual Report for 1979, p.116.

Table 1-10. Fertility of pollen and spikelet in F$_1$s between Aus varieties and Indica or Japonica testers (TARC, Okinawa, 1981 - 83)

Variety	Source	Fertility of variety %		F$_1$-fertility %			
				With a Japonica tester		With an Indica tester	
		Pollen	Spikelet	Pollen	Spikelet	Pollen	Spikelet
Test with Akihikari and IR 36 as a Japonica and an Indica tester, respectively, in 1981.							
Achar Bhog	Acc. 25826	97.4	81.5 (98)	78.0	71.1 (83)	75.1	62.0 (79)
Aus 371	Acc. 29157	96.7	86.0 (98)	97.9	64.2 (80)	93.2	38.1 (45)
Aus 402	Acc. 29186	98.1	86.8 (92)	55.6	59.8 (68)	98.8	85.1 (93)
Aus 430	Acc. 29212	99.6	55.4 (93)	53.2	41.5 (60)	69.9	46.0 (69)
DZ 151	Acc. 8541	98.5	62.5 (90)	72.2	22.2 (36)	59.0	70.2 (82)
DV 16	Acc. 8812	97.4	62.8	85.5	19.1 (24)	90.4	70.2 (83)
Test with Akihikari and IR 50 as a Japonica and an Indica tester, respectively, in 1982.							
Aus 373	Acc. 29158	99.4	92.8	94.3	88.0	89.6	91.3
Dharial	CAES	97.2	—	75.7	32.8	76.8	22.4
Test with Akihikari and IR 36 as a Japonica and an Indica tester, respectively, in 1983.							
DJ 123	Acc. 8455	98.3	95.7	93.0	87.2	69.4	70.9
DV 149	Acc. 8538	96.6	83.8	49.8	85.1	94.2	86.1
Ingra	Acc. 27552	98.8	97.8	48.2	61.6	97.4	68.3
CH 972	200011	97.2	80.0	58.2	30.5	94.7	84.8
CH 1039	200033	98.1	85.6	58.4	13.2	98.2	96.3
R 11	200035	99.4	85.2	97.9	88.5	85.8	62.3
Kaladumai	200040	99.5	93.0	94.0	94.7	58.4	81.1
Dular	200041	96.6	94.0	97.1	83.7	89.6	86.7
Katakutara	200048	97.2	87.0	66.4	86.9	57.6	43.1
Parambu Vattan	200049	99.5	89.2	98.6	89.1	28.7	34.0
N 136	200052	97.4	91.0	92.9	36.8	87.4	70.8
Marichi Buti	200059	95.8	85.0	81.5	61.5	74.2	50.0
Jhanji	200061	97.2	90.9	85.4	60.8	96.2	93.7
Sataka	210003	96.2	91.2	96.1	81.8	83.3	54.4
Kele	210013	98.0	82.2	54.2	69.4	92.2	88.2
Bhutmari 36	210014	98.6	91.7	95.8	53.5	87.6	93.2
Marichibati	CAES	94.4	79.2	98.2	90.8	86.4	48.1

Source number with "Acc." is from IRRI and that with six digits from NIAS.
Figures in parentheses indicate maximum spikelet fertility of ten samples. In other cases the spikelet fertility is a mean from two or three visually good panicles.

4. Aus Varieties

Test of compatibility type. By the end of 1983, 25 varieties were crossed to an Indica as well as to a Japonica tester to determine the pollen and spikelet fertility of the F_1 hybrids (Table 1-10). Besides, two others were included in the preliminary test, the results of which were published earlier (Ikehashi and Araki). In 1984, 14 varieties were added to the compatibility test, and the results are listed in Table 1-11. Thus, a total of 41 Aus varieties was tested. All the data are listed in Appendix I together with some other characteristics of the varieties. In Appendix I, all the varieties are re-arranged in the order of compatibility. Owing to the lack of some noted Aus varieties,

Table 1-11. Fertility of pollen and spikelet in F_1s between Aus varieties and Indica or Japonica testers (TARC, Okinawa, 1984)

Variety	Source	Fertility of variety %		F_1-fertility %			
				With a Japonica tester		With an Indica tester	
		Pollen	Spikelet	Pollen	Spikelet	Pollen	Spikelet
Test with Akihikari and IR 36 as a Japonica and an Indica tester, respectively, in 1983.							
Borlun	Acc. 27534	97.0	93.4	49.5	64.9	82.7	88.4
Chakila	Acc. 27540	99.3	96.7	53.2	77.5	92.9	89.8
Porang	Acc. 27577	98.4	97.1	96.7	52.3	45.4	67.3
DV 32	Acc. 8818	97.9	96.7	83.8	93.7	48.1	35.4
DV 34	Acc. 8820	98.7	93.2	69.9	84.0	67.5	54.8
DV 52	Acc. 8828	95.8	96.7	81.1	91.8	68.4	83.7
H 2871	200001	99.4	96.9	95.8	93.1	44.5	35.8
M 142	200014	97.8	99.3	99.6	94.3	44.8	70.3
AS 20-1	200022	97.4	99.1	84.5	89.1	90.8	77.2
RDR 7	200027	100.0	93.2	91.3	92.1	40.7	26.5
AS 35	200028	98.9	97.8	70.0	94.4	89.6	91.3
Lepudumai	200044	97.9	76.3	71.0	93.3	49.9	80.0
Charnock	200060	96.3	82.0	48.6	32.1	92.5	39.5
Kumari	210004	99.2	95.6	59.6	69.8	92.3	93.4

Table 1-12. Fertility of F_1 hybrids between Aus varieties and testers, in second season, 1985 (Additional data)

Tester varieties	Aus varieties					
	Karalath		Pusur		Surjamkhi	
	Pollen%	Spikelet%	Pollen%	Spikelet%	Pollen%	Spikelet%
Japonica						
Akihikari	92.6	91.7	46.1	85.1		
Tatsumimochi					88.1	96.2
Indica						
IR 36	73.4	77.2	77.7	91.1		
IR 50					30.4	41.4
Ketan Nangka	59.0	58.8	52.2	47.2	95.1	91.2
Aus varieties						
Panbira	99.7	91.6	98.4	95.0		
Achar Bhog					79.6	83.1

Testers are used as pollinators except for Surjamkhi, which was used as a female parent.

three Aus varieties were later added to the compatibility test in 1985 (Table 1-12).

Two varieties, Aus 373 and Dular seemed to be widely compatible, although the pollen fertility in their cross to IR varieties was marginal. Next to these two, five varieties, i.e. Akula, AS 35, DV 145, Panbira and Bhutmari 36 showed fertility except in one of the four fertility tests. Seven varieties, i.e. Aus 402, CH 972, CH 1039, Chakila, Jhanji, Kele and Kumari showed normal fertility with the Indica testers, but lower fertility with the Japonica tester. Contrastingly, nine varieties, i.e. DJ 123, H 2871, Kaladumai, M 142, Marichibati, Paramb Vattan, R 11, RDR 7 and Satika showed normal fertility with the Japonica tester, but lower fertility with the Indica tester.

The rest of the 18 varieties were not classified into any definite categories. Out of them, five varieties, Achar Bhog, Aus 430, Dharial and Marichi Buti showed incompatibility with Indica and Japonica testers. In many cases the compatibility for these varieties were marginal, leaving some possibility of re-classification. Contrastingly, the fertility values in typical Indica-Japonica crosses were clearly differentiated from the marginal values.

Table 1-13. Fertility of F$_1$s between Aus varieties, 1984 - 85

	A.373	Dular	DV149	Panb.	Bhut.	CH972	Kele	DJ123	Kal.	P.Va.	Sati.	Ingra	A.Bh.
Aus 373		98.8	93.9	96.4	93.2		94.8	96.8		72.8	98.0	97.0	98.2
Dular	94.7		96.7	97.2	83.5	100	98.9	94.5	98.9	94.3	98.0	98.8	97.0
DV 149	96.4	90.8			89.8	86.4	95.1	99.2	97.5		97.7	98.6	91.1
Panbira	91.4	94.9			97.5	69.6	95.0			67.4	96.3	89.4	99.3
Bhutmari 36	93.3	94.6	96.4	98.2		87.3			97.0		99.3	97.7	57.8
CH 972		96.8	91.4	72.3	84.6		93.0	95.1	81.6	78.4	93.1	99.3	70.0
Kele	94.0	100	100	94.9				94.8		19.0	99.6	98.4	97.1
DJ 123	94.3	97.3	98.5			68.5	94.1		94.1	50.6	94.2	97.0	94.4
Kaladumai		98.7	100		100	87.6		100				100	99.3
Prambu Vattan	72.4	96.4		74.2		54.0	23.9	85.0			82.5	51.1	71.1
Satika	100	92.2	98.7	95.7	94.0	96.4	91.3	95.1		86.4		99.6	98.0
Ingra	79.4	94.7	91.9	93.2	91.5	62.0	84.7	92.0	87.2	76.6	98.0		99.2
Achar Bhog	92.5	93.0	93.9	94.5	77.4	88.5	92.7	98.6	91.7	97.5	98.4	89.0	

Above diagonal pollen fertility, below diagonal spikelet fertility, respectively, in percentage.

Crosses among Aus varieties. In the compatibility test of the Aus varieties, there were different types of compatibility in the Aus varieties; some were like Indicas and other like Japonicas. Therefore, some varieties from different compatibility types in the Aus group were chosen, and crosses were made among them to test the fertility of the F$_1$ hybrids. The results are shown in Table 1-13. The data in the Table are a summary of the crosses made for the two years, and the description of the female and male varieties for each of the crosses is not specified. To determine the extent of environmental or reciprocal differences, some cases of reciprocal crosses are shown in Table 1-14. From the Table, it seems that reciprocal difference were not observed except in the pollen fertility of Achar Bhog/DJ 123. As pollen fertility is subject to

Table 1-14. **Fertility of F_1 hybrids of reciprocal crosses between Aus varieties**

Crosses	Test of	Fertility %	
		Pollen	Spikelet
Achar Bhog/Aus 373	1984. I	94.0	94.1
Aus 373/Achar Bhog	1984. I	98.2	97.5
Achar Bhog/DJ 123	1984. I	58.2	82.3
DJ 123/Achar Bhog	1984. II	94.4	98.6
CH 972/Ingra	1984. I	94.8	51.4
Ingra/CH 972	1984. I	99.3	62.0
Dular/Satika	1985. I	98.0	92.2
Satika/Dular	1985. I	98.6	100

Table 1-15. **Fertility of F_1 hybrids between wide-compatibility varieties and Aus varieties**

Cross or varieties	Fertility %	
	Pollen	Spikelet
Tests in 1983		
Panbira	98.3	80.0
IR 36/Panbira	87.6	92.1
Taichung 65/Panbira	71.3	51.7
Ketan Nangka/Pnabira	55.0	74.7
Panbira/Ketan Nangka*	75.6	19.9
Achar Bhog	96.8	91.4
IR 36/Achar Bhog	86.4	92.6
Akihikari/Achar Bhog	86.1	72.4
Ketan Nangka/Achar Bhog	53.1	60.5
Achar Bhog/Ketan Nangka*	93.0**	55.6
Tests in 1984		
Ketan Nangka/Achar Bhog	56.9	75.1
Achar Bhog/Ketan Nangka	40.6	59.2
Ketan Nangka/Panbira	34.9	70.6
Panbira/Ketan Nangka	41.3	18.1
Tests with Calotoc and CPSLO 17 in 1983		
Panbira/CPSLO 17	66.4	68.6
Panbira/Calotoc	88.2	47.1
DZ 151/CPSLO 17	71.5	68.8
DZ 151/Calotoc	93.8**	75.8
Achar Bhog/CPSLO 17	83.3	83.9
Achar Bhog/Calotoc	93.6**	81.8
Aus 430/CPSLO 17	87.5	83.2
Aus 430/Calotoc	93.3**	79.7

Notes : * Tests in following season.
** Levels of fertility were overestimated due to the occurrence of small empty pollen.

environmental differences or seasonal changes, further evaluation is needed to confirm the reciprocal difference. Generally, the fertility of the hybrids was normal regardless of the compatibility types of the parent variety. An exeptionally low fertility was sometimes observed in the crosses of a variety, Prambu Vattan. This variety was similar to Japonica varieties in various aspects, and seemed to be unique in the Aus group. It can be concluded that the F_1 hybrids between any two Aus varieties exhibit a generally normal fertility.

Crosses between Aus varieties and Javanica varieties (WCV). Initially, some Aus varieties were crossed to WCVs and the fertility of the F_1 hybrids was examined (Table 1-15). In all the cases, these F_1 hybrids showed a lower fertility. During the first observation of pollen fertility, many empty pollen samples were excluded from the counting, and the resulting fertility was calculated to be as high as about 90 percent. But, further testing showed that the pollen fertility was very low in these F_1 hybrids. It was interesting to note that the F_1 hybrids between Ketan Nangka and Panbira showed clear reciprocal differences in spikelet fertility.

To determine whether the lower fertility is a general phenomenon in the F_1 hybrids between WCVs and Aus varieties, some more Aus varieties were crossed to Ketan Nangka, and in some cases to other Javanica varieties. It was shown that the F_1s gave a lower fertility with a few exceptions (Table 1-12 and 1-16). In terms of spikelet fertility of F_1 hybrids, Dular, Kaladumai and Pramb Vattan showed good compatibility with Ketan Nangka. And, Surjamukhi showed a somewhat high fertility with Ketan Nangka (Table 1-12).

Table 1-16. Fertility of F_1s between Javanica and Aus varieties (Additional data, 1984 - 85)

Aus varieties	Javanica varieties (%)					
	Ketan Nangka		Banten		Penuh Baru II	
	Pollen	Spikelet	Pollen	Spikelet	Pollen	Spikelet
Achar Bhog	(Table	1-15)	68.2	39.1	32.7	48.6
Aus 373	55.6	50.1[1]	82.4	24.0	93.4	58.6
Bhutmari 36	55.2	42.5[1]				
CH 972	61.3	65.3[2]			43.6	50.0
DJ 123	53.5	57.9[1]	40.7	64.4		
Dular	56.6	90.9[5]	92.8	89.6	78.7	73.1
DV 149	64.7	79.3[1]				
DZ 151	41.9	79.7[2]				
Ingra	51.9	48.8[2]	58.8	85.5		
Kaladumai	77.9	97.5[2]			93.5	89.2
Kele	48.8	22.6[3]	74.4	50.0		
Panbira	(Table	1-15)	46.7	25.0	44.6	44.6
Prambu Vattan	80.9	92.4[3]	87.6	81.4	42.7	54.7
Satika	65.7	60.1[4]			59.4	40.0

Note : 1) Test in first season, 1984 as Aus pollinator
2) Test in second season, 1984 as Ketan Nangka pollinator
3) Test in first season, 1985 as Ketan Nangka pollinator
4) Test in first season, 1985 as Aus pollinator
5) Test in second season, 1984 as Aus pollinator
Penuh Baru II and Banten were all crossed as pollinators, and tested in 1985.

Earlier, it was indicated that the Penuh Baru Group of Javanica and some Aus varieties such as Achar Bhog were similar to each other with regard to their incompatibility both with the Indica and Japonica testers, however, F_1 hybrids between the Penuh Baru Group of Javanica varieties and some Aus varieties such as Achar Bhog showed a very low compatibility (Table 1-17).

Table 1-17. Fertility of F_1 hybrids between 'Penuh Baru' group of Javanica varieties and Aus varieties (1983 - 84)

Cross or varieties	Fertility %	
	Pollen	Spikelet
Panbira	98.3	80.0
Panbira/simanuk	78.2	47.7
Panbira/Penuh Baru II	72.8	16.0
Panbira/Sigabe Taon	42.5	35.7
Panbira/Page Leoh*	35.4	9.3
Achar Bhog	98.5	89.4
Achar Bhog/Simanuk	79.5	58.0
Achar Bhog/Penuh Baru II	60.6	21.4
Achar Bhog/Sigabe Taon	60.7	35.4
Achar Bhog/Page Leoh	54.9	77.7
DV 16	97.3	90.0
DV 16/Simanuk	49.4	28.7
DV 16/Penuh Baru II**	52.2	13.3
DV 16/Page Leoh	72.0	55.4
DV 16/Sigabe Taon*	59.4	4.7
Aus 373	98.3	94.2
Aus 373/Page Leoh	66.4	79.8
Aus 373/Penuh Baru II*	67.1	43.8
Aus 373/Sigabe Taon*	58.6	43.8
Aus 373/Simanuk*	76.5	64.6
Aus 371	95.5	86.1
Aus 371/Simanuk	70.1	77.7
Aus 371/Page Leoh	76.4	76.8
Control for the tests in 1984		
Panbira	98.2	84.5
DV 16	92.7	88.1
Aus 373	96.8	94.0

Note : * Tests in 1984.

5. South Indian or Sri Lanka varieties

Triveni and Eat Samba were not definitely classified into Indicas nor into Japonicas like other varieties, Dahanala and Pokkali. In this context, these varieties from South India or Sri Lanka seemed to be similar to some of the Aus varieties. In another series of tests, Triveni, Eat Samba and Dahanala were crossed to Ketan Nangka, and the F_1 hybrids showed a lower fertility (Table 1-18). This fact also suggests that these three varieties are similar to the Aus varieties. The F_1 hybrid between Triveni and Achar Bhog showed normal fertility confirming the similarity of the South Indian varieties and Aus varieties.

Table 1-18. Compatibility types of Peta and some varieties from South India or Sri Lanka

Cross or varieties	Fertility %	
	Pollen	Spikelet
Peta	100	
IR 50/Peta	100	84.8
Akihikari/Peta	59.0	55.0
Taichung 65/Peta	84.5	61.4
Triveni	98.3	75.6
IR 36/Triveni	85.9	85.7
Akihikari/Triveni	67.0	38.7
Triveni/Achar Bhog*	93.2	98.6
Triveni/Ketan Nangka*	30.8	37.9
Eat Samba	100	
IR 50/Eat Samba	90.3	85.9
IR 36/Eat Samba	81.7	87.5
Akihikari/Eat Samba	91.8	90.7
Ketan Nangka/Eat Samba	77.8	49.9
Dahanala		
IR 36/Dahanala	75.8	74.3
Taichung 65/Dahanala	55.4	33.2
Nihonmasari/Dahanala	64.6	45.0
Ketan Nangka/Dahanala	85.2	67.6

Note : * Tests in 1985.

6. Some varieties from Bhutan, China and Korea.

Two improved Korean lines and Nanjing 11 seemed to be of the Indica type. It was worth noting that the Korean lines showed a slightly lower pollen fertility with Ketan Nangka. A similar lower pollen fertility was observed when IR 36 was pollinated to Ketan Nangka. Some Chinese native varieties were similar to Indicas, but differed in their lower fertility with Ketan Nangka. Nanjing 11 seemed to be a typical Indica except for a slightly lower pollen fertility with the Indica tester. Two of the Bhutan varieties, Jyakuchem and Kuchem showed good fertility both with Indica and Japonica testers, suggesting their wide compatibility (Table 1-19, 20).

Table 1-19. Pollen and spikelet fertility in F_1 hybrids between testers and Korean or Chinese varieties

Testers	Varieties crossed as pollinators (%)											
	Milyang 23		Suweon 258		Pi-bi-hun		Tuan-ku-chao		Tao-jen-chiao		Nanjing 11	
	Poll.	Spik.	Poll.	Spik.	Poll.	Spik.	Poll.	Spik.	Poll.	Spik.	Poll.	Spik.
Akihikari	45.3	38.5	40.4	44.8	65.1	41.7*	79.1	37.9	43.5	12.5**	39.3	48.5
IR 36	83.4	85.5	58.3	86.5	99.0	93.7	92.9	89.2	97.7	94.9	95.2	82.1
Ketan Nangka	86.2	96.8	77.0	92.8	71.5	44.8	—	—	75.9	44.8	96.1	94.8
CPSLO 17	93.2	97.5	92.0	95.4	—	—	—	—	—	—	60.7	94.5
Achar Bhog	63.5	64.6	63.0	87.8	66.7	74.2	68.8	83.3	77.4	57.8	93.0	89.7
Aus 373	90.9	—	66.8	93.6	52.8	86.5	87.5	98.4	89.5	97.1	71.8	93.6

Note: * Taichung 65 was used instead of Akihikari.
** Tatsumimochi was used instead of Akihikari.

Table 1-20. Fertility of F_1 hybrids between Bhutan varieties and testers, second season in 1985

Testers	Bhutan varieties (%)							
	Jyadwmjya		Dumjya		Jyakuchem		Kuchem	
	Poll.	Spik.	Poll.	Spik.	Poll.	Spik.	Poll.	Spik.
Tatsumimochi	65.3	82.5						
Akihikari					84.9	90.2	92.8	89.7
IR 36	93.7	96.0	62.7	97.5	91.7	94.3	86.9	90.5
Achar Bhog					88.4	84.1	72.1	71.4
Padi Bujang Pendek					53.8	82.3	97.8	77.2

All the Bhutan varieties were used as pollinators.

Discussion

The number of samples of the present test was very small in view of innumerable number of varieties, but significantly larger than that in previous studies, which included only several varieties from each group. As a result, it was possible to reveal the diversity of the compatibility types in each group.

Javanica varieties. The term 'Javanica' was redefined by Morinaga (1954) for the Indonesian native varieties, 'Bulu' (awned) or 'Gundil' (awnless), and recognized as a varietal group different from the varietal group, 'Tjereh', which is of the Indica type. The comparative characteristics of these varietal groups were described earlier by Van der Meulen (1941). Matsuo (1952)'s description of Bulu was in good agreement with Van der Meulen's. Later, Morinaga (1958, 1968) used the name Bulu instead of Javanica. But, no comprehensive local term is known for bulu and gundil in Indonesia.

Thus, it seems better to call this varietal group Javanica group.

The characteristics of the Javanica varieties can be related to their adaptability to upland cultivation. The thick stems with longer, droopy leaves and large panicles are common traits in upland varieties which require thick and deep roots. The lack of photoperiod-sensitivity and very long basic vegetative growth also characterize upland rices in the tropics, where a long growth period is essential to attain a certain amount of growth before flowering.

It is interesting to note that the three WCVs, i.e. Calotoc, Ketan Nangka and CPSLO 17 can be included into the Javanica group. CPSLO 17 with its short, tillering plant type is not a typical Javanica. But, its wide compatibility can be traced back to Philippine native varieties through one of its parent, Century Patna 231, which was derived from a cross of Texas Patna//Rexoro/Supreme Blue Rose (a Japonica variety) and noted for its wide compatibility with Peta, Sigadis, BPI 76, Taichung Native 1 (Jennings, 1966). Texas Patna's parents and Rexoro are Philippine native varieties (IRRI, 1979). Terao and Mizushima (1939) reported that Ketan Nangka showed a normal fertility in its cross to Tetep (a typical Indica variety) and to three Japnese varieties.

Besides the WCVs, five types of compatibility were found in the Javanica group. Out of them, the majority of the varieties belong to the 'Banten' group, which exhibited fertility with the Japonica tester and spikelet semi-sterility with the Indica tester. In the initial test of Javanica varieties, no Japonica type was found, however, Hawara-Geporeck in the preliminary test and two photoperiod-nonsensitive varieties in the test of stress-tolerant varieties, i.e. Kinandang Patong (a well known donor of drought tolerance) and Paedai Kuribungga were morphologically of the Javanica type, and compatible with the Japonica tester but not with the Indica tester.

In the stress-tolerant varieties, many varieties from the Philippines or Indonesia were typically of the Indica type, showing clear semi-sterility with Japonicas and normal fertility with Indicas. At the same time, they are strongly photoperiod-sensitive, in contrast to the Javanica varieties. Photoperiod-sensitivity is an essential trait for traditional lowland rice cultivation, and an important criterion to separate Indonesian and Philippine native varieties into two groups. The sensitive group is likely to be of the Indica type known as Tjereh, and the nonsensitive one belongs to Javanica group, the compatibility of which is characterized by the Banten group, WCVs, Penu Baru II group, and Japonica types. Chang (1976) assumed that Javanica varieties are derivatives of Indica rice. But, the compatibility tests showed that Javanica varieties are close to Japonica varieties, and they include the compatibility of the Japonica type as a component.

With regard to the fertility of F_1 hybrids between different groups in the Javanica varieties, normal fertility was observed except in the case of Saba Enim. The reproductive barrier is not clearly developed within the Javanica varieties despite their differential compatibility with Indica and Japonica testers. It is of particular interest that all of these compatibility types including the Indica and Japonica types show normal fertility with the WCVs. In this context, they all can represent a group of varieties with a link to the WCVs.

Aus varieties. In the earlier works, differences between Aus varieties and typical Indica and Japonica varieties were reported, and they were recognized as an intermediate group between Indica and Japonica subspecies (Terao and Mizushima, 1939; Morinaga and Kuriyama, 1958).

In the present study, the diversity of compatibility types within this group was revealed with the Indica and Japonica testers. Varietal diversity was also indicated in other traits, such as alkali-digestion, phenol reaction, heariness of glumes, cold tolerance, and so on. Some Aus varieties were found to be similar to Indicas and others to Japonicas. It was noteworthy that Dular showed an exceptionally good compatibility with Indica, Javanica and Japonica varieties. This is in good agreement with the observation by Morinaga and Kuriyama (1958).

However, the F_1 hybrids between different compatibility types of the Aus varieties generally showed a good level of fertility. In this context, the Aus group is similar to the Bulu group. And the Indica-like or Japonica-like types in the Aus varieties cannot be Indica or Japonica varieties in terms of their compatibility. Furthermore, it was shown that many of the Aus varieties exhibited clear F_1 sterility with Ketan Nangka and other WCVs. The wide compatibility of the WCVs seemed to be effective for the Indica, Javanica and Japonica varieties but not for the Aus varieties.

From these evidences, the Aus varieties as a whole seem to be different from the Indica, Japonica and Javanica varieties, as indicated by other workers. In connection with this, it should be noted that some native or improved varieties from the South Indian region showed similarity to Aus varieties with respect to their F_1 sterility with Ketan Nangka and to their marginal compatibility with Indica or Japonica testers. In the tests by Terao and Mizushima (1939), Ketan Nangka showed a somewhat lower compatibility with two Aus varieties, Surjamukhi and Mushakudanchi, and apparent incompatibility with Dahanala. Although the number of varieties tested is too limited to draw a firm conclusion, it is suggested that the rice varieties in the South Indian region are likely to be of the Aus type in terms of their compatibility. Originally, the term Aus is for photoperiod-nonsensitive summer varieties in the Bengal region of the Indian Subcontinent. But, the compatibility of the Aus type can be widely found among the varieties in the Indian Subcontinent.

Summary

A total of 80 varieties, most of which are Aus or Bulu varieties, were crossed to an Indica and a Japonica tester variety, and the four fertility criteria for each variety, i.e. the pollen and spikelet fertility of the F_1 hybrids with the Indica or Japonica tester was examined to determine the compatibility type of each variety.

In the initial test, Calotoc, Ketan Nangka and CPSLO 17 were confirmed to be 'compatible' with Indica as well as Japonica varieties.

Out of 24 Indonesian varieties, a majority of 15 varieties (Banten and Gamah group) were classified into one group by their high pollen fertility both with the Indica and Japonica tester, the normal spikelet fertility with the Japonica tester, and the clear semi-sterility with the Indica tester. Six varieties (Penuh Baru group) showed sterility with both of the testers. Only one variety, Padi Bujang Pendek revealed a normal fertility in its hybrids with the Indica and Japonica testers. One variety, Hawarageporeck tested in the preliminary trial seemed to be of the Japonica type.

The F_1 hybrids between different compatibility types in the Javanica group showed generally a normal fertility with a few exceptions like Saba Enim.

Out of 14 varieties tolerant of environmental stress, Kinandan Patong and Paedai Kulibungga were not photoperiod-sensitive, and their compatibility was found to be of the Japonica type. All the other varieties of this group were strongly photoperiod-sensitive except for the variety Palar, a weakly sensitive one. The majority of ten

varieties with strong photoperiod-sensitivity were found to be of the Indica type.

In the test of Aus varieties, two varieties, Aus 373 and Dular seemed to be widely compatible, although the pollen fertility in their cross to IR varieties was marginal. Next to these two, five varieties showed fertility except in one of the four fertility criteria. Seven varieties showed a normal fertility with the Indica tester, but a lower fertility with the Japonica tester. Contrastingly, nine varieties showed a normal fertility with the Japonica tester, but a lower fertility with the Indica tester. The remaining 18 varieties were not classified into any definite category. In many cases the compatibility for these varieties were marginal, leaving a possibility for re-classification.

With a few exceptions, the fertility of the hybrids between two Aus varieties was found to be normal regardless of the compatibility types of the parent variety.

In the hybrids between some Aus varieties and WCVs (wide-compatibility varieties) the fertility of the F_1 hybrids was very low with a few exceptions, Dular and other two Aus varieties which showed good compatibility with Ketan Nangka. In the additional tests of varieties from South India, Sri Lanka, Bhutan, China and Korea, some varieties from South India were not definitely classified into Indicas or into Japonicas. The F_1 hybrids between them and Ketan Nangka showed a lower fertility. It was suggested that these varieties are similar to the Aus varieties. Two improved Korean lines and Nanjing 11 were seemed to be of the Indica type. Two Bhutan varieties, Jyakuchem and Kuchem showed good fertility both with Indica and Japonica testers, suggesting a wide compatibility.

The varietal group of Aus includes various compatibility types in terms of F_1 sterility, and the types of compatibility are likely to be different from Indica, Javanica, and Japonica types.

II. Genetic analyses of F_1 sterility in distant crosses

The partial F_1 sterility due to gamete abortion was once ascribed to structural differences between the chromosomes of Indica and Japonica types as reviewed by Chandraratna (1964). In the past three decades the sterility in distant crosses has been mainly ascribed to genic differences. However, there are two contrasting genetic explanations.

Oka (1953, 1964, 1974) proposed a model of duplicate recessive gametophytic lethals, assuming that the genotypes of gametic lethals for two distantly related varieties, A and B are Xy/Xy and xY/xY, respectively, and such gamates as concurrently carrying recessive lethals, x and y on the F_1 hybrid of Xy/xY become aborted due to some deficiency of gamete development factors. Varieties producing fertile hybrids, when crossed to A as well as to B, were assumed to be of XY/XY genotype. In this paper such a variety is called a wide-compatibility variety (WCV). Oka's hypothesis was

Table 2-1. Design to test two theoretical models for hybrid sterility by means of marker genes

Common premise for two models:

Wide-compatibility variety (WCV) produces fertile F_1, when crossed to variety A or to B. F_1 from A/B is semi-sterile.

Model I: Sterility is caused by allelic interaction.

Assumed genotypes:

S^n/S^n for WCV with S^n linked to dominant marker genes;

S^a/S^a and S^b/S^b, respectively for variety A and B.

Expression of F_1 genotypes:

S^n/S^a and S^n/S^b are fertile; S^a/S^b is semi-sterile.

Linkage between marker and fertility in three-variety cross

Test cross	Produced genotypes	Linkage between marker and fertility
WCV/A//B	S^n/S^b (fert.) + S^a/S^b (semi-st.)	detectable
WCV/B//A	S^n/S^a (fert.) + S^b/S^a (semi-st.)	detectable

Model II: Sterility is caused by duplicate recessive lethals.

Assumed genotypes:

X^wY/X^wY for WCV with X^w linked to dominant marker genes;

Xy/Xy and xY/xY, respectively for variety A and B.

Expression of F_1 genotypes

F_1 genotype of Xy/xY shows semi-sterility due to abortion of gamete carrying duplicate recessive lethal genes, xy.

Linkage between marker and fertility in three-variety cross

Test cross	Produced genotypes	Linkage between marker and fertility
WCV/A//B	X^wY/xY (fertile) X^wy/xY (semi-sterile) XY/xY (fertile) Xy/xY (semi-sterile)	not detectable
WCV/B//A	X^wY/Xy (fertile) X^wY/Xy (fertile) xY/Xy (semi-sterile) xY/Xy (semi-sterile)	detectable

based on data obtained from a three-variety cross of A//WCV/B. According to Oka (1953) a cross of A//WCV/B, the genotype of which can be written as Xy//XY/xY, segregated fertile (XY/xY) and semi-sterile (Xy/xY) progenies in a ratio of 1:1. The result was interpreted as the evidence of duplicate gametic lethals (Model II in Table 2-1).

Kitamura (1962, 1963) reported contrasting results in which female and male gametes were independently aborted by respective allelic interaction. It was assumed that Indica and Japonica varieties posses Fs^{i}/Fs^{i} and Fs^{j}/Fs^{j} alleles (*Female semi-sterility*), respectively, at a locus, and the gametes carrying Fs^{j} were aborted in the maternal genotype of Fs^{i}/Fs^{j}. In this system, the genotype for WCVs can be given as Fs^{n}/Fs^{n}, assuming that Fs^{n}/Fs^{i} and Fs^{n}/Fs^{j} are fertile (Model I in Table 2-1). Although Kitamura had never reported the type of WCVs, the existence of such varieties was indicated in the preceding Chapter. As the second step, the genetic nature of the WCVs was investigated.

Materials and Methods

Four groups of varieties were used as shown in Table 2-2: (1) three WCVs identified in the screening, (2) Indica testers, IR 36 and IR 50, (3) six Japonica varieties and (4) three Javanica varieties. All of the WCVs tested possess *C* (Chromogen for pigmentation) and *A* (Anthocyanin activator gene). In rice plants, *C* and *A* complementarily determine pigmentation, and *P* (distributor gene) which locates the pigmentation at the apiculus is known to exist widely, and in all the varieties in the present experiment.

Initially, to test the validity of the proposed models, three-variety crosses were designed to detect linkage between the marker genes and pollen or spikelet fertility in the pair cross scheme as shown in Table 2-1.

Table 2-2. Marker genes of tested varieties

Varietal groups	Varieties	Linkage group		
		I	II	III
Widely compatible variety	Ketan Nangka	*alk*, *C*, *wx*	Ph^{+}, *Ps*	*A*
	Calotoc	+, *C*, +	Ph^{+}, Ps^{+}	*A*
	CPSLO 17	+, *C*, +	Ph^{+}, Ps^{+}	*A*
IRRI	IR 36, IR 50	+, C^{+}, +	*Ph*, *Ps*	*A*
Japonica variety	Akihikari	*alk*, C^{+}, +	Ph^{+}, Ps^{+}	A^{+}
	Tohoku 127			
	Nihonmasari			
	Kochihibiki			
	Taichung 65	*alk*, *C*, +	Ph^{+}, Ps^{+}	A^{+}
	Hata-koganemochi	*alk*, C^{+}, *wx*	Ph^{+}, Ps^{+}	A^{+}
Javanica variety	Banten	+ *C*, +	Ph^{+}, Ps^{+}	A^{+}
	Gamah			
	Penuh Baru II	+, C^{+}, +	Ph^{+}, *Ps*	*A*

According to the two-locus model, the assumed genotype for WCVs is XY/XY, and the genotype for distantly related varieties A and B is Xy/Xy and xY/xY, respectively. Then the role of X and Y from a WCV can be differentiated from each other in the paired crosses, WCV/A//B and WCV/B//A as indicated in the model II of Table 2-1. If X^w of a WCV is effective for fertility in WCV/B//A, the effect of X^w can not be detected in WCV/A//B, and *vice versa*. In other words, if the variety with xY gametes is crossed lastly, progeny plants with Y from WCV should reveal fertility and those with y be semi-sterile, whereas, if the varieties with Xy gametes are crossed lastly, the progenies with X from WCV should show fertility and those with x be semi-sterile. Therefore, if one of the dominant genes, X or Y of a WCV is linked with some marker genes, the linkage between the marker and the fertility level should be detected only in one of the paired crosses.

Contrastingly, if the fertility is controlled by one-locus system, the effect of WCV's S^n gene should be detected in both of the paired crosses (Model I in Table 2-1). If the S^n gene is linked with a marker, the linkage between the fertility and the marker of the

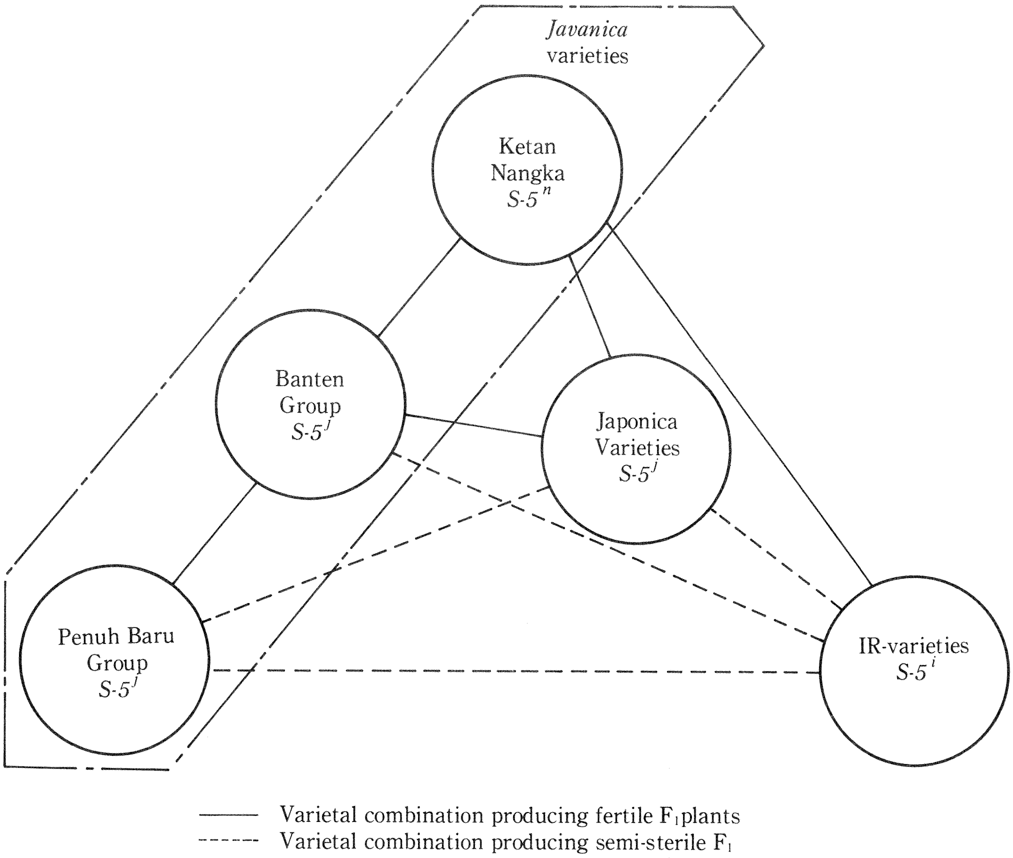

Fig. 1. F_1 fertility and pertinent alleles in the crosses between Indica, Javanica and Japonica varieties.

The compatibility in terms of spikelet sterility indicated here agrees with the compatibility in terms of pollen fertility except that the F_1 of Banten group/IR-varieties exhibits normal pollen fertility.

S^n can be detected in both of the paired three-variety crosses.

After preliminary tests, the *C* gene was found to be a key marker. The paired three-variety crosses were made primarily with a WCV, Ketan Nangka which possesses three markers, i.e. *alk* (alkali digestion), *C* and *wx* (waxy endosperm) in the linkage group I. The Indica testers and WCVs have *A*, and only WCVs have *C*, while the Japonica varieties except Taichung 65 have none of these (Table 2-2). Accordingly, any progeny plants possessing *C* from the WCVs were able to be detected by the presence of apiculus pigment in the three-variety crosses.

As the first experiment suggested the validity of the one locus model, it was expected that those gametes carrying S^i or S^j should be aborted in the F_1 genotype of S^i/S^j, thereby showing distorted segregation of the markers. To test the occurrence of such gamete abortion, F_1 hybrids of the Japonica variety/IR 36 were backcrossed with IR 36.

Javanica varieties were added to the experiments. The results of the former experiment showed that the majority of Javanica varieties was identified as Banten type, and six as Penuh Baru II type, which showed semi-sterility when crossed to Indica as well as to Japonica testers. Both types produced fertile F_1s when crossed to Ketan Nangka (Fig. 1). Penuh Baru II was tested in the paired three-variety cross of Ketan Nangka/Penuh Baru II//IR 50 and Ketan Nangka/IR 36//Penuh Baru II. Banten and Gamah from the Banten group of Javnica varieties were added to the gamete abortion tests.

For each of the three-variety crosses, 50-60 F_1 plants were grown in an irrigated field at the Okinawa Branch, TARC. The pollen and spikelet fertilities were recorded for each plant by standard procedures.

Results

1. Evidence of allelic interaction for spikelet fertility in Indica-Japonica crosses

The implication of three-variety crosses. The distribution of spikelet fertility in the paired three-variety crosses, i.e. Akihikari/Ketan Nangka//IR 36 and IR 36/Ketan Nangka//Akihikari is given in Table 2-3. It was previously confirmed that Ketan Nangka is a WCV, and the F_1 hybrids between IR 36 and Akihikari show semi-sterility. In the cross of Akihikari/Ketan Nangka//IR 36, the genotype of *wx*/+ and C/C^+ clearly showed a significantly higher fertility than the reverse genotype, +/+ and C^+/C^+. In the cross of IR 36/Ketan Nangka//Akihikari, the relationship between the fertility and the marker genotypes was also found, although it was not as clear as in the former cross.

Two reasons for the weak linkage between the marker and the fertility in IR 36/Ketan Nangka//Akihikari can be indicated.

Firstly, a genic interference was found to be associated with *Ph*. In that cross, the difference in the fertility between *wx*/+ and +/+ and that between C/C^+ and C^+/C^+ was clear in the presence of the *Ph* gene (Table 2-4). The *Ph*-related effect seems to have affected all the genotypes in Akihikari/Ketan Nangka//IR 36, since the donor of the *Ph* related effect was IR 36. And this cross revealed clear differences in the fertility between the reverse marker genotypes.

Secondly, different frequencies of genic recombination were observed between the paired crosses. The recombination value between *C* and *wx* was higher in IR 36/Ketan

Table 2-3. Distribution of spikelet fertility in three-variety crosses with wide-compatibility variety, Ketan Nangka

Marker genes	No. of plants in each fertility class										Total	Mean	t-test
	-10	-20	-30	-40	-50	-60	-70	-80	-90	-100 %		%	
Akihikari/Ketan Nangka//IR 36 (1983)													
C/C^{+}							8	12	9		29	75.8	**
C^{+}/C^{+}				2	4	8	7	1	2		24	57.2	
$wx/+$				1		1	10	12	9		33	73.1	**
$+/+$				1	4	7	5	1	2		20	57.9	
IR 36/Ketan Nangka//Akihikari (1983)													
$wx/+$			1	5	4	2	6	5	2	1	26	59.2	
$+/+$		2	4	3	2	4	3	2	3		23	49.9	
C/C^{+}			1	4	4	2	2	5	4	1	23	60.9	*
C^{+}/C^{+}		2	4	4	2	4	7	2	1		26	49.4	
alk/alk			1	3	3	2	3	2	5	1	20	62.1	*
$alk/+$		2	4	5	3	4	6	5			29	49.8	
Ph/Ph^{+}		2	3	5	3	3	6	6	3	1	32	55.6	
Ph^{+}/Ph^{+}			2	3	3	3	3	1	2		17	53.4	
IR 36/Ketan Nangka//Tohoku 127 (1981)													
C/C^{+}	4	1	5	4	3	4	8	7	4	3	43	54.1	*
C^{+}/C^{+}	2	7	2	10	3	5	2	3	2		36	40.7	
Ph/Ph^{+}	3	5	3	5	2	3	6	5	3	3	38	49.7	
Ph^{+}/Ph^{+}	3	3	4	9	4	6	4	5	3		41	46.4	
Kochihibiki//IR 36/Ketan Nangka (1981)													
$wx/+$		1	1	1	3	8	8	8	6	2	38	65.6	
$+/+$			1	2	2	10	3	4	4	3	29	63.4	
C/C^{+}			1		1	5	5	9	9	5	35	73.8	**
C^{+}/C^{+}		1	1	3	4	13	6	3	1		32	54.6	
alk/alk			2		3	6	4	7	8	5	35	70.0	**
$alk/+$		1		3	2	12	7	5	2		32	58.8	
Ph/Ph^{+}		1			3	13	7	6	3	4	37	64.7	
Ph^{+}/Ph^{+}			2	3	2	5	4	6	7	1	30	64.6	
IR 36/Ketan Nangka//Taichung 65 (1984)													
$wx/+$		1	1	2	4	3	4	7	10	1	33	66.0	
$+/+$			3	2	3		3	3	3	2	19	58.8	
alk/alk		1	1	1	1	1	1	5	9	1	21	70.6	*
$alk/+$			3	3	6	2	6	5	4	2	31	58.5	
Ph/Ph^{+}			2		4	3	3	3	7		22	63.1	
Ph^{+}/Ph^{+}		1	2	4	3		4	7	6	3	30	63.6	

*, ** : Significant at 5% and 1%, respectively.

Table 2-4. Spikelet fertility classified by *Ph* gene and other marker genes

Marker genotype	No. of plants in each fertility class -20	-30	-40	-50	-60	-70	-80	-90	-100 %	Total	Mean %	t-test
					IR 36/Ketan Nangka//Akihikari (1983)							
Ph/Ph^+, *wx*/+		1	2	2	1	4	4	2	1	17	62.8	*
Ph/Ph^+, +/+	2	2	3	1	2	2	2	1		15	47.4	
Ph^+/Ph^+, *wx*/+			3	2	1	2	1			9	52.4	
Ph^+/Ph^+, +/+		2		1	2	1		2		8	54.6	
Ph/Ph^+, C/C^+			2	2	1	1	4	3	1	14	64.4	**
Ph/Ph^+, C^+/C^+	2	3	3	1	2	5	2			18	47.2	
Ph^+/Ph^+, C/C^+		1	2	2	1	1	1	1		9	52.4	
Ph^+/Ph^+, C^+/C^+		1	1	1	2	2		1		8	54.6	
Ph/Ph^+, *alk/alk*			2	1	1	2	1	3	1	11	61.6	
Ph/Ph^+, *alk*/+	2	3	3	2	2	4	5			21	50.1	
Ph^+/Ph^+, *alk/alk*		1	1	2	1	1	1	2		9	57.5	
Ph^+/Ph^+, *alk*/+		1	2	1	2	2				8	48.8	
					Kochihibiki//IR36/Ketan Nangka (1981)							
Ph/Ph^+, *wx*/+	1			1	4	4	3	2	1	16	65.3	
Ph/Ph^+, +/+				2	9	3	3	1	3	21	64.2	
Ph^+/Ph^+, *wx*/+		1	1	2	4	4	5	4	1	22	65.8	
Ph^+/Ph^+, +/+		1	2		1		1	3		8	61.0	
Ph/Ph^+, C/C^+					2	2	3	3	4	14	77.4	**
Ph/Ph^+, C^+/C^+	1			3	11	5	3			23	57.0	
Ph^+/Ph^+, C/C^+		1		1	3	3	6	6	1	21	71.4	**
Ph^+/Ph^+, C^+/C^+		1	3	1	2	1		1		9	48.6	
Ph/Ph^+, *alk/alk*				1	3	3	3	3	4	17	72.8	**
Ph/Ph^+, *alk*/+	1			2	10	4	3			20	57.8	
Ph^+/Ph^+, *alk/alk*		2		2	3	1	4	5	1	18	67.3	
Ph^+/Ph^+, *alk*/+			3		2	3	2	2		12	60.4	

*, ** : Significant at 0.05% and 0.01%, respectively.

Nangka than in Akihikari/Ketan Nangka (Fig. 2). This fact implies that the recombinations between the marker genes and the gene for the fertility were more frequent in IR 36/Ketan Nangka than in Akihikari/Ketan Nangka. The higher recombination frequency explains the weakened linkage between the markers and the fertility in IR 36/Ketan Nangka//Akihikari. Recombination values in distant crosses are often larger than those in crosses within a varietal group (Omura, 1981).

Although there were such modifying factors, the linkage between the markers and the fertility was clearly shown in both of the paired crosses. This fact supports the one-locus model illustrated in the Table 2-1. Therefore, the fertility must be contrlled by the S^n gene from Ketan Nangka, the locus of which seemed to be linked closely with *C*.

The results of additional three-variety crosses are shown in Table 2-3. In the 1981 tests of Kochihibiki//IR 36/Ketan Nangka, a clear differentiation of the fertility levels was shown between the marker genotypes, i.e. C/C^+ versus C^+/C^+ and *alk/alk* versus *alk*/+. As Kochihibiki is the same kind of Japonica variety as Akihikari and can not be different from Akihikari in terms of compatibility with IR 36, the effect of the marker genotype on the level of the spikelet sterility was reconfirmed in the cross of Japonica//IR 36/Ketan Nangka.

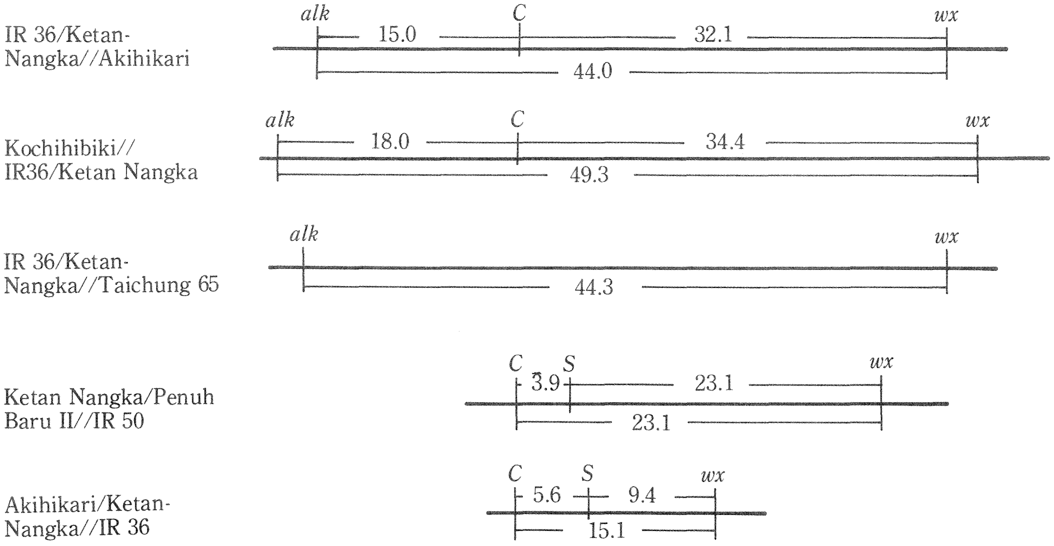

Fig. 2. Intensity of linkage among some markers in the Linkage Group I and assumed locus of *S*-alleles, allelic interaction of which caused semi-sterility of spikelet.

Additional evidences for one-locus model. The results of additional three-variety crosses with Calotoc or CPSLO 17 are presented in Table 2-5, where IR 36/Calotoc//Akihikari and Nihonmasari/Calotoc//IR 36 similarly showed a close linkage between the *C* gene and spikelet fertility. As the two Japonica varieties are known to behave identically in distant crosses, these crosses with Calotoc give additional evidence that the segregation of fertility is basically controlled by one locus (Model I in Table 2-1). In the crosses with Calotoc and CPSLO 17, the *Ph*-related interference was not observed (Table 2-6). From the data in Table 2-6, CPSLO 17 was assumed to have the same gene as Calotoc and Ketan Nangka. Therefore, all the three WCVs seem to have a common S^n gene at the same locus near *C*.

Table 2-5. Distribution of spikelet fertility in three-variety crosses with Calotoc and CPSLO 17

Marker genes	No. of plants in each fertility class -20	-30	-40	-50	-60	-70	-80	-90	-100 %	Total	Mean %	t-test
					IR 36/Calotoc//Akihikari (1983)							
C/C^+		1		3	2	5	10	5	3	29	70.7	**
C^+/C^+	1	1	5	11	7	3				28	45.6	
Ph/Ph^+		1	2	9	6	4	2	4	3	31	60.4	
Ph^+/Ph^+	1	1	3	5	3	4	8	1		26	54.4	
					Akihikari//IR 36/Calotoc (1983)							
C/C^+			1		1	5	10	13	1	31	76.7	**
C^+/C^+		2	3	12	5	8	2			32	51.1	
Ph/Ph^+		1		8	3	9	7	12		40	66.7	*
Ph^+/Ph^+		1	4	4	3	4	5	1	1	23	58.4	
					Nihonmasari/Calotoc//IR 36 (1981)							
C/C^+	1	2	2	2	8	3	3	2	1	24	56.4	**
C^+/C^+	7	7	9	8	4	3		1		39	36.3	
					IR 36//Nihonmasari/Calotoc (1982)							
C/C^+					2	3	8	10	4	27	79.5	**
C^+/C^+		1	5	5	7	6	2	1		27	53.5	
					CPSLO 17/IR 36//Nihonmasari (1983)							
C/C^+			2		1	5	4	6	1	19	70.7	**
C^+/C^+			3	5	9	8	2	2		29	57.4	
Ph/C^+			2	3	6	9	4	7		31	64.9	
Ph^+/Ph^+			3	2	4	4	2	1	1	17	58.5	

*, ** : Significant at 0.05% and 0.01%, respectively.

Table 2-6. Spikelet fertility classified by *Ph* gene and other marker genes

Marker genotype	No. of plants in each fertility class -30	-40	-50	-60	-70	-80	-90	-100 %	Total	Mean %	t-test
				IR 36/Calotoc//Akihikari							
Ph/Ph^+, C/C^+			2	1	2	2	4	3	14	75.3	**
Ph/Ph^+, C^+/C^+	1	2	7	5	2				17	48.1	
Ph^+/Ph^+, C/C^+	1	1	1	1	3	7	1		15	63.8	**
Ph^+/Ph^+, C^+/C^+	1	3	4	2	1				11	41.8	
				Akihikari//IR 36/Calotoc							
Ph/Ph^+, C/C^+				1	4	6	12		23	77.7	**
Ph/Ph^+, C^+/C^+	1		8	2	5	1			17	51.9	
Ph^+/Ph^+, C/C^+		1			1	4	1	1	8	73.6	**
Ph^+/Ph^+, C^+/C^+	1	3	4	3	3	1			15	50.2	
				CPSLO 17/IR 36//Nihonmasari							
Ph/Ph^+, C/C^+		1			4	3	6		14	73.4	**
Ph/Ph^+, C^+/C^+		1	3	6	5	1	1		17	58.0	
Ph^+/Ph^+, C/C^+		1		1	1	1		1	5	62.9	
Ph^+/Ph^+, C^+/C^+		2	2	3	3	1	1		12	56.7	

*, ** : Significant at 0.05% and 0.01%, respectively.

Test of gamete abortion by the frequency of marker gene. The results of the test crosses are shown in Table 2-7. In the cross of Hata-kogane-mochi/IR36//IR36 and Taichung 65/IR36//IR36, the frequencies of the B_1F_1 plants carryign *wx, alk* or *C* were significantly decreased. Despite the small sample size, the same tendency was observed in the cross of Taichung 65/Milyang 23//Milyang 23. These facts indicated that a part of the gametes carrying the allele from the Japonica parent, S^j was aborted in the F_1 genotype of S^i/S^j.

In all the three crosses listed in Table 2-7, there were some plants which carried the marker gene of Indica varieties but showed a clear semi-sterility. This kind of individual plants may be the recombinants between the marker gene and the S^j gene. With regard to the loci of *S* and *C* in the F_1 hybrid, because the donor of *C* is Taichung 65, a Japonica variety, there should have been four kinds of female gametes, i.e. C-S^j and C^+-S^i in the original linkage and C^+-S^j and C-S^i in the recombined status. All the gametes which survived were fertilized by C^+-S^i gametes of IR 36, so that four kinds of genotypes were produced in the B_1F_1 of Japonica/IR 36//IR 36, i.e. CS^j/C^+S^i, C^+S^i/C^+S^i, C^+S^j/C^+S^i and CS^i/C^+S^i. The majority of the female gametes carrying S^j must have been eliminated, and the number of the recombinant gametes must have been limited, therefore, the ratio of the four kinds of gametes can be illustrated, as shown in Fig. 3. In the cross of Taichung 65/IR36//IR36, if fertile plants are defined by a fertility level higher than 75 percent, the ratio of the four kinds of B_1F_1 gametes can be determined. The intensity of the *C-S* linkage and the survival rate of gametes with S^j are determined as shown in Figure 3.

Table 2-7. Female-gamete elimination and its effect on spikelet fertility detected in Japonica/Indica//Indica crosses

Marker genes	No. of plants in each fertility class -40	-50	-60	-70	-75	-80	-85	-90	-95	-100%	Total	Mean %	t-test
						Taichung 65/Milyang 23//Milyang 23 (1983)							
C/C^+				1			4		1		6	82.1	**
C^+/C^+				1			1	2	10	4	18	91.0	
alk/+				2			2		2	2	8	85.6	
+/+							3	2	9	2	16	90.4	
						Hata-kogane-mochi/IR 36//IR 36 (1983)							
wx/+			5	6	2	2	2	1			18	67.9	**
+/+				4	5	5	8	3	3		28	79.1	
alk/+			3	4	1						8	61.4	**
+/+			2	6	6	7	10	4	3		38	77.5	
						Taichung 65/IR 36//IR 36 (1984)							
C/C^+	3		3	7		3	8	3			27	69.6	**
C^+/C^+				3	3	12	20	14	15		67	83.9	
alk/+	3		2	7		6	9	5	1		33	72.8	**
+/+			1	3	3	9	19	12	14		61	83.6	

*, ** : Significant at 0.05% and 0.01%, respectively.

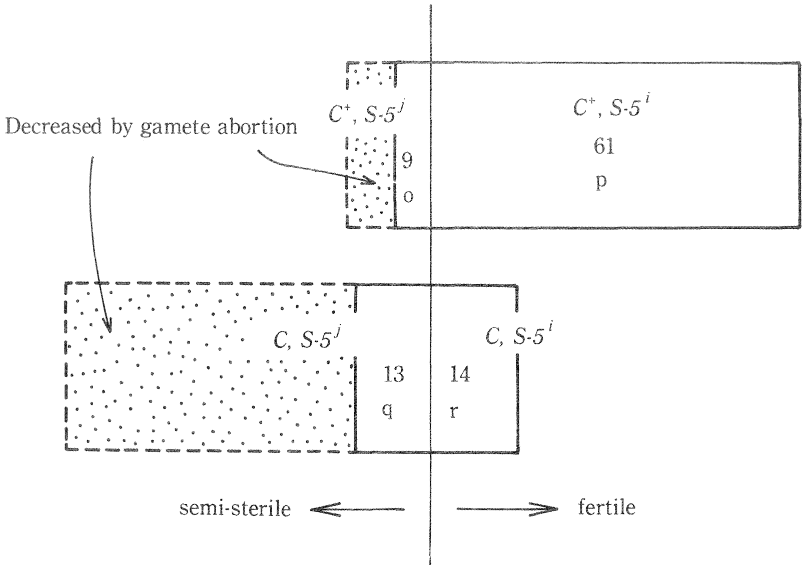

Fig. 3. Estimation of gametes which survived or were aborted in the F_1 of $S\text{-}5^i/S\text{-}5^j$ (Taichung 65/IR 36)

Survival rate of $S\text{-}5^j$ gametes: (o+q)/(p+r) = 19/75 = 0.25
Recombination value between C and $S\text{-}5$: r/(p+r) = 0.18

2. Three-variety cross for Indica-Javanica crosses

Table 2-8. Distribution of spikelet fertility in three-variety crosses with Ketan Nangka, Penuh Baru II

Marker genes	No. of plants in each fertility class -30	-40	-50	-60	-70	-80	-90	-100%	Total	Mean %
				Ketan Nangka/Penuh Baru II//IR 50 (1984)						
C/C^+			1			7	16	3	27	82.1
C^+/C^+	1	2	7	14			1		25	50.9
wx/+			2	3		6	13	1	25	76.5
+/+	1	2	6	11		1	4	2	27	58.5
				Ketan Nangka/IR 36//Penuh Baru II (1985)						
C/C^+				2	1		12	42	57	91.7
C^+/C^+		3	26	21	6	2			58	52.1
wx/+			2	9	2	1	9	29	52	83.3
+/+		3	24	14	5	1	3	13	63	61.4
				Ketan Nangka/Akihikari//Penuh Baru II (1985)						
C/C^+	3		1	3	14	15	23	4	63	73.7
C^+/C^+			5	2	9	11	15	6	48	74.2
wx/+	3		3	3	15	16	21	5	66	73.4
+/+			3	2	8	10	17	5	45	76.2

Three variety crosses with Javanica varieties. Javanica varieties were classified into several compatibility types (Fig. 1). Out of them Penuh Baru II and other three varieties were found to give semi-sterile F_1 hybrids when crossed to the Japonica and Inidca testers, but completely fertile F_1 in the cross to Ketan Nangka. In the three variety-cross of Ketan Nangka/Penuh Baru II//IR 50, close linkages were found between the spikelet fertility and *wx* or *C* gene from Ketan Nangka (Table 2-8). The paired cross, namely, Ketan Nangka/IR 36//Penuh Baru II, which was later tested in 1985, also clearly showed the same linkage relationship (Table 2-8). Therefore, Ketan Nangka's S'' allele which is closely linked with the marker must be allelic to the sterility-causing allele in the F_1 between Indica and Javanica varieties. Since the F_1 hybrids between Penuh Baru II and Indica are semi-sterile, the allele possessed by Penuh Baru II must be diferent from S^i. On the other hand, the F_1 sterility between Penuh Baru II and Japonica varieties did not seem to be affected by the locus near *C* and *wx* in the related cross of Ketan Nangka/Akihikari//Penuh Baru II, which did not show the linkage relationship between the *S* locus and the sterility (Table 2-8).

Based on these results, the compatibility relation among Indica, Javanica and Japonica varieties can be ascribed to an allelic interaction of the multiple alleles at the *S* locus as shown in Fig. 1. However, the sterility of F_1 between Penuh Baru II and Akihikari seems to be caused by allele at another unknown locus.

Table 2-9. Distribution of spikelet fertility in Javanica/IR 50//IR 50 and Javanica/IR 50//Taichung 65

Marker genotype	No. of plants in each fertility class								Total	Mean %	
	-30	-40	-50	-60	-70	-80	-90	-100%			
				Banten/IR 50//IR 50 (1983)							
C/C^+			1	2	5	3			11	63.8	
C^+/C^+			2	2	6	14	12	6	42	76.5	
total			3	4	11	17	12	6	53	73.9	
				Banten/IR 50//Taichung 65							
A/A^+	1	3	7	6	1	2	2		22	53.7	**
A^+/A^+		4	6	7	4	2			23	54.0	
Ph/Ph^+		4	8	8	2	1			23	51.4	
Ph^+/Ph^+	1	3	5	5	3	3	2		22	56.4	
total	1	7	13	13	5	4	2		45	53.9	
				Gamah/IR 50//IR 50							
C/C^+				5	4	2	1		12	65.2	
C^+/C^+				7	8	9	8	2	34	72.2	
total				12	12	11	9	2	46	70.3	
				Gamah/IR 50//Taichung 65							
A/A^+			3	2	1				6	51.5	**
A^+/A^+	2	1	4	5	3				15	49.8	
Ph/Ph^+	2		2	3	2				9	48.1	
Ph^+/Ph^+		1	5	4	2				12	51.9	
total	2	1	7	7	4				21	50.3	

*, ** : Significant at 0.05% and 0.01%, respectively.

Gamete elimination test for Indica-Javanica crosses. In the compatibility test of Javanica varieties, a majority of the group showed compatibility with Japonicas but not with the Indica tester in terms of spikelet sterility. These varieties were represented by Banten and Gamah, which produced fertile F_1 hybrids when crossed to Penuh Baru II. To identify the alleles possessed by Banten and Gamah, B_1F_1 of Banten or Gamah/IR50//IR50 were tested for their marker gene and fertility (Table 2-9). Based on the results, it was shown that a portion of the gametes with the *C* of Banten was eliminated in the F_1 of Banten/IR 50, as it was in the Indica-Japonica cross (Table 2-7). The same result was obtained in the cross of Gamah. The elimination of the gametes carrying *C* indicates that Banten and Gamah may have an allele which behaves like the Japonica's S^j.

Gamete elimination test for the F_1 hybrid between a Japonica variety and Penuh Baru II. To identify the gamete genotype which may be eliminated in the semi-sterile F_1 hybrid between Japonica varieties and Penuh Baru II, a backcrossed progeny was tested in the cross of Kamairazu/Penuh Baru II//Kamairazu. Kamairazu is of a Japonica type in terms of compatibility with other groups of varieties (Table 3-4), and has a marker gene, *bc* (brittle culm) in the XIth linkage group. In the backcrossed progeny, the plants having two marker genes, *alk* near the *S-5* locus and *bc* were able to be distinguished.

The results are shown in Table 2-10. In terms of the marker genes, there was no difference in the frequency of *bc/bc* or *alk/alk* gamete against the opposite allele. It was difficult to relate the F_1 sterility to the allelic interaction at a locus near the two loci. This finding is in accordance with the result of Ketan Nangka/Akihikari//Penuh Baru II, where allelic interaction at the *S-5* locus was not suggested. Therefore, it is suggested

Table 2-10. Distribution of pollen and spikelet fertility in the cross of Kamairazu/Penuh Baru II//Kamairazu

Genotype	No. of plants in each fertility class								Total	Mean
	-30	-40	-50	-60	-70	-80	-90	-100 %		%
			Spikelet fertility							
bc/bc	1	4	2	5	2	4	7	8	33	70.3
bc/+	1		3	3	6	9	6	8	36	73.9
alk/+	2	3	4	4	2	7	6	10	38	70.5
alk/alk		1	1	4	6	6	7	6	31	74.3
bc/bc, alk/+	1	3	1	1	1	3	3	4	17	68.0
bc/bc, alk/alk		1	1	4	1	1	4	4	16	72.9
bc/+, alk/+	1		3	3	1	4	3	6	21	72.6
bc/+, alk/alk					5	5	3	2	15	75.8
			Pollen fertility							
bc/bc	1	2	4	1	1	8	4	12	33	75.6
bc/+		3	6	5	7	2	5	8	36	67.9
alk/+	1	1	4	5	4	5	5	13	38	74.1
alk/alk		4	6	1	4	5	4	7	31	68.5
bc/bc, alk/+	1		1	1		5	2	7	17	78.7
bc/bc, alk/alk		2	3		1	3	2	5	16	72.4
bc/+, alk/+		2	3	4	4		3	6	21	70.3
bc/+, alk/alk		2	3	1	3	2	2	2	15	64.4

that Akihikari and Penuh Baru II may possess the same allele at the *S-5* locus. This assumption is reasonable, as some of the Javanica varieties showed the same compatibility type as the Japonicas, and the allele of Banten at the *S-5* behaved like $S\text{-}5^j$ in the gamete elimination test (Table 2-9). The suggested allelic relation is shown in Fig. 1.

3. Mapping of the *S* locus

Since the distribution of the spikelet fertility was continuous and subject to environmental fluctuations, the recombinants between the *S* locus and the markers were not easily determined. However, in one cross with Penuh Baru II (Table 2-8), the distribution of spikelet sterility was clearly separated into low and high groups. Hence, the recombination values were calculated, as shown in Fig. 2. In another cross of Akihikari/Ketan Nangka//IR 36, clear linkage between the fertility and two markers was shown, so that the progeny plants underlined in Table 2-3 were tentatively assumed to be recombinants. Thus, calculated recombination values showed good fitness with the value between *wx* and *C* (Fig. 3).

4. Pollen fertility and the marker gene

In all of the previous experiments, although pollen fertility was recorded for individual plants, no relationship was found between the sterility and the marker genotypes. Therefore, the data for the pollen sterility were excluded from the present record.

Discussion

The experimental results showed that the one-locus model is valid and a set of multiple alleles was identified; S^n for WCVs, S^i and S^j for Indica and Japonica varieties, respectively. The allelic interaction of S^i/S^j was shown to cause partial abortion of gametes carrying S^j. This system can be called one-locus sporo-gametophytic interaction after Oka (1974). A similar case was described in tomato by Rick (1966). Sano *et al.* (1979) reported a case of gamete abortion by allelic interaction in the crosses between isogenic lines from an Indica variety of *Oryza sativa* and a strain derived from *Oryza glaberrima*. As the identification of the *S* locus with those reported earlier, from *S-1* to *S-4*, by Sano *et al.* (1979) and Sano (1983a, 1983b) in interspecific hybrids was not undertaken, the present locus is to be tentatively designated hereafter as *S-5*.

It is noteworthy that the experimental results which Oka (1953) initially cited as an evidence for the two-locus model can also be interpreted by a one-locus model, as shown in Table 2-1. Oka's experiment (1953) gave a single case of ambiguous implication. Nevertheless, the two-locus model had been widely accepted before Oka's additional work in 1974. Oka (1974) reported his experiments with isogenic lines which were derived from distantly related varieties, and supported his theory of the two-locus model. But, it should not be overlooked that Oka's explanation of the results was based on hypothetical competitive fertilization of pollen genotypes, and that most of the experimental results can also be explained by the one locus-model without postulating such competitive fertilization. According to the one locus model, the F_1 between two genotypes, Xy/Xy and xY/xY should give the fertility level of 75 percent. Actually in the Oka's test of F_1 between the isogenic lines, the genotype of which was expected to be Xy/xY, the observed fertility was 40–60 percent against the expected fertility of 75 percent. On the other hand, Kitamura's induction of one-locus model was based on extensive tests of isogenic lines.

For the practice of breeding, the two models predict contrasting outcome from a distant cross. According to the two-locus model, a cross showing F_1 sterility may eliminate a majority of "recessive lethal genes" from its progeny, and ultimately produce many lines which would behave like WCV. The one-locus model envisages that only one of the parent alleles can be predominant in the progeny, and that the WCV type can not be expected. Thus, the understanding of the nature of the F_1 sterility is not only related to varietal differentiation of rice but also to basic strategies of rice breeding.

Through the extensive tests of Indica-Japonica crosses in Japan, it has been realized that the fertility level in Indica/Japonica//Japonica backcrosses is apparently lower than in Indica/Japonica//Indica backcrosses. This can be explained by the elimination of $S\text{-}5^j$ in the first cross, and not reasonably predicted by the two-locus model which assumes a symmetrical genotype for each component of the Indica/Japonica crosses.

From the view point of the one-locus model, an antagonism between the heterozygous maternal tissue and the gametes carrying one of the alleles must be the basis for F_1 sterility. The mutation at the *S-5* locus seems to produce new alleles which are antagonistic to each other, and to develop reproductive barriers. When F_1 sterility is not observed between two varieties, there should be two possibilities: each of their allele is identical to each other; or one of them is a neutral one like $S\text{-}5^n$.

The difference of alleles between Japonica and Javanica varieties is not determined. The F_1 between Penuh Baru II and a Japonica variety showed sterility, but it was based on a locus other than the *S-5*. The diversity of the *S-5* locus in Indica and Japonica was demonstrated by the identification of some alleles. Of these, the role of S^i is of interest, because it eliminates the opposite allele together with adjacent genes, and forms an exclusive set of traits. In practice, the exclusion of the *alk-wx* segment of Japonica or Javanica varieties in the hybrids with Indicas should be taken into account, as these genes determine the cocking quality of rice.

Throughout the present study, pollen fertility was recorded, but no link was found between the fertility and the markers.

Summary

The F_1 sterility in wide crosses of cultivated rices has been explained by two contrasting genetic models: A model of duplicate recessive gametophytic lethals (two-locus model) assumes that the genotypes of gametic lethals for two distantly related varieties, A and B are Xy/Xy and xY/xY, respectively, and such gametes as concurrently carrying recessive lethals, x and y on the F_1 hybrid of Xy/xY become aborted due to the deficiency of gamete development factors; According to another model (one-locus model), it is assumed that Indica and Japonica varieties possess Fs^i/Fs^i and Fs^j/Fs^j alleles, respectively, at a locus, and the gametes carrying Fs^j were aborted in the maternal genotype of Fs^i/Fs^j. In this system, the genotype for WCVs can be given as Fs^n/Fs^n, assuming that Fs^n/Fs^i and Fs^n/Fs^j are fertile.

To test the validity of the proposed models, three-variety crosses were designed to differentiate the role of two independent putative genes, X and Y. Ketan Nangka as a WCV, an Indica tester (IR 36), and a Japonica tester (Akihikari) were crossed. The cross of IR 36/Akihikari was confirmed to show partial sterility. In the cross of Akihikari/Ketan Nangka//IR 36, the genotype, *wx*/+ and C/C^+ clearly showed a significantly higher fertility than the contrasted genotype, +/+ and C^+/C^+. In the cross of IR 36/Ketan Nanngka//Akihikari, the same linkage between the fertility and the marker genotypes was found. The two marker genes *wx* and *C* are known to be closely linked, and possessed by Ketan Nangka. Therefore, the fertility was assumed to be controlled by the S^n gene from Ketan Nangka. The three-variety crosses with Calotoc or CPSLO 17 similarly showed the close linkage between the *C* gene and spikelet fertility. It was concluded that all the three WCVs have a common S^n gene at the same locus near *C*, which was named *S-5*. On the basis of the one-locus model, it was expeted that such gametes as those carrying $S\text{-}5^i$ from an Indica variety or $S\text{-}5^j$ from Japonica should be aborted in the semi-sterile genotype of $S\text{-}5^i/S\text{-}5^j$, thereby showing distorted segregation of the markers. The experimental results indicated that a majority of the gametes carrying the allele from the Japonica parent, $S\text{-}5^j$ was aborted in the F_1 genotype of $S\text{-}5^i/S\text{-}5^j$.

Ketan Nangka's $S\text{-}5^n$ allele was also found to be effective for the sterility in the F_1 between Indica testers and Javanica varieties, such as Banten and Penuh Baru II. In the F_1 between an Indica tester and Javanica testers, Banten and Gamah, a majority of the gametes with *C* of Banten or Gamah was found to be eliminated. This fact indicated that Banten and Gamah may have an allele which behaves like the Japonica's $S\text{-}5^j$. As a whole, the compatibility relation among Indica, Javanica and Japonica varieties was ascribed to an allelic interaction of the multiple alleles at the *S-5* locus. However, the F_1 sterility between Penuh Baru II, a Javanica variety and Japonica varieties seemed to be caused by an allele at another locus than the *S-5*.

In one cross with Penuh Baru II, the distribution of spikelet sterility was clearly separated into low and high groups. Hence, the recombination values were estimated. In another cross of Akihikari/Ketan Nangka//IR 36, the celar linkage between the fertility and the marker genes indicated the *S-5* locus between *wx* and *C*.

III. Pollen fertility and so-called gametophyte genes

In all of the experiments with the three-variety crosses with WCVs, pollen fertility was recorded, but no marker gene was related to the pollen fertility. However, some results showed indirectly the genic behavior of the pollen fertility.

Firstly, the effect of the WCV's wide compatibility in terms of pollen fertility was traced through several steps of repeated hybridization. As a result, a genic effect similar to that reported by Kitamura (1962, 1963) was suggested: Sc^i (scanty pollen) for Indica variety and Sc^j for Japonica. And, the gametes carrying Sc^j seemed to be aborted in the genotype of Sc^i/Sc^j. This model seemed to be a basis for the analysis of pollen sterility, selective fertilization or abortion of gametes. This finding led us to retest of some marker genes which were reported to be linked with gametophyte genes. The behavior of the marker genes which were linked with duplicate recessive gamete lethals by Oka (1974) was also retested in relation to pollen fertility.

Materials and Methods

Tracing of wide-compatibility genes by three-variety crosses. The F_1 hybrids between wide compatibility varieties such as Calotoc and Ketan Nangka on one hand and Indica or Japonica testers on the other hand were confirmed to show normal pollen fertility (Chap. I). Accordingly, a series of experiments was designed to trace the wide compatibility, as shown in Table 3-1.

Table 3-1. Experiment to trace WCV's 'Wide Compatibility Gene' for pollen fertility

Gene symboles:

Fs^n: WCV's 'wide compatibility' gene for pollen fertility

Fs^i: Indica's pollen fertility gene (after Kitamura (1962))

Fs^j: Japonica's pollen fertility gene (after Kitamura (1962))

Actual Crosses	Assumed genotypes
Ketan Nangka (KN) as WCV:	
IR 36/KN	Fs^i/Fs^n (fertile)
IR 36/KN//Tohoku 127 (TH) (Japonica)	$Fs^i/Fs^n//Fs^j/Fs^j$
	= $Fs^i/Fs^j + Fs^n/Fs^j$ (fertile)
IR 36///IR 36/KN//TH	$Fs^i/Fs^i//Fs^n/Fs^j$
	= $Fs^i/Fs^j + Fs^i/Fs^n$ (fertile)
Akihikari////IR 36///IR 36/KN//TH	$Fs^j/Fs^j//Fs^i/Fs^n$
	= $Fs^j/Fs^i + Fs^j/Fs^n$ (fertile)
Calotoc (CT) as WCV:	
Nihonmasari (NM)/Calotoc	Fs^j/Fs^n (fertile)
IR 36//NM/CT	$Fs^i/Fs^i//Fs^j/Fs^n$
	= $Fs^i/Fs^j + Fs^i/Fs^n$ (fertile)
NM///IR 36//NM/CT	$Fs^j/Fs^j//Fs^i/Fs^n$
	= $Fs^j/Fs^i + Fs^j/Fs^n$ (fertile)
IR 36////NM///IR 36//NM/CT	$Fs^i/Fs^i//Fs^j/Fs^n$
	= $Fs^i/Fs^j + Fs^i/Fs^n$ (fertile)

Only pollen-fertile progeny was pollinated in successive crosses.

Firstly, the progeny from Indica/Ketan Nangka//Japonica (Tohoku 127) or Indica//Japonica/Calotoc was confirmed to segregate a certain number of plants with normal pollen fertility. The fertile plants are supposed to carry the WCV's gene. Then, those pollen-fertile plants from the cross of Indica/Ketan Nangka//Japonica were crossed to the Indica tester (IR 36) as polinator. Likewise, the pollen-fertile plants from the cross of IR 36//Japonica/Calotoc were crossed to the Japonica tester (Nihonmasari) as pollinator. Out of the progeny of these crosses, the pollen-fertile plants were further crossed as pollinator to the respective tester, as shown in Table 3-1.

If the WCV had such a wide compatibility gene as found for spikelet fertility, there should be at least a number of pollen-fertile plants after each of the crosses.

Test of pollen-fertility genes with the use of marker-gene-lines. In the second experiment, Japonica testers with additional marker genes, i.e. *lg* (liguleless in the second linkage group), and *bc* (brittle culm) and *lop*-2 (dl-lopped leaf -2) of the XI linkage group were tested in addition to *alk, C, Ph* and so on. These testers were provided by Prof. Omura of Kyushu University. Oka (1974) assumed the presence of recessive lethal genes for pollen fertility which were linked to *wx, lg* and *bc*. And, Nakagahra *et al.* (1972), and Nakagahra (1972) reported the presence of gametophyte genes closely linked to *bc* and *dl* genes. Some experimental Japonica lines with these markers were crossed to Indica testers, and the relation between these markers and pollen or spikelet fertility was examined.

Results

Tracing of wide-compatibility gene for pollen fertility. The results of the first series of the experiments are shown in Table 3-2 and 3-3. In 1981, the progeny of the three-variety crosses showed a group of pollen-fertile individual plants. In the Ketan Nangka crosses, the ratio of pollen-fertile plants with a fertility level of 90–100% was not different between the crosses, i.e. IR 36/Ketan Nangka//Tohoku 127 and Kochihibiki//IR 36/Ketan Nangka. These two crosses are practically reciprocal, because Tohoku 127 and Kochihibiki are typical Japonica varieties. For the Calotoc crosses, some confirmation tests were repeated in 1982. The cross of IR 36/Calotoc//Kochihibiki segregated a larger number of fertile plants than its reciprocal, Kochihibiki//IR 36/Calotoc. Similarly, IR 36//Nihonmasari/Calotoc segregated a larger number of fertile plants than its reciprocal, Nihonmasari/Calotoc//IR 36. As the reciprocal difference in the F_1 hybrids between the Japonica/Indica and Indica/Japonica was not significant (Table 3-2), the reciprocal difference in the three-variety crosses can be related to some other factors than cytoplasmic effect.

Further, some pollen-fertile progeny plants were crossed to the tester as pollinator in 1981. The fertility of the progeny of those crosses is shown in the upper part of Table 3-3. In the Ketan Nangka crosses, approximately half of the progeny plants showed a nearly normal fertility, while a majority of the progenies in Calotoc crosses was semi-sterile. Some fertile plants from these progenies were crossed again to the testers, and the fertility of the progenies was tested in 1983 (Table 3-3). In the Ketan Nangka crosses, half of plants was fertile, whereas, in the Calotoc crosses, a majority of the progenies was fertile.

The ratio of fertile *versus* semi-sterile plants changed significantly in the Calotoc crosses. When the Indica tester was used as female plants, the majority of the

Table 3-2. **Pollen fertility of progeny from three-variety crosses with WCVs**

Marker	No. of plants in each fertility class -40	-50	-60	-70	-80	-90	-100 %	Total	Mean %
1981									
IR 36/Ketan Nangka//Tohoku 127									
C	1	2	1	1	7	7	25	44	85.4
C$^+$	2	1	5	9	4	9	18	48	77.3
Kochihibiki//IR 36/Ketan Nangka									
C		2	1	2		8	21	34	88.4
C$^+$		2	1	3	2	4	19	31	85.7
Nihonmasari/Calotoc//IR 36									
C					1	13	10	24	89.2
C$^+$	1			3	3	13	19	39	87.0
IR 36//Nihonmasari/Calotoc									
C				1	1		3	5	86.0
C$^+$				1		2	9	12	92.6
Control									
NM/IR 36			1	6	15	7		29	75.3
1982									
IR 36/Calotoc//Kochihibiki									
C		1	4	4	2	8	7	26	76.1
C$^+$	1	1	1	2	5	8	10	28	81.4
Kochihibiki//IR 36/Calotoc									
C	4	4	3	3	4	1	1	20	57.1
C$^+$	2	1	2	3	4	1		13	61.0
IR 36//Nihonmasari/Calotoc									
C				1	3	7	16	27	89.1
C$^+$				2	2	10	13	27	88.3
Nihonmasari/Calotoc//IR 36									
C *C*$^+$	1	1	2	13	13	29	23	82	82.1
Control									
NM/IR 36		3	6	2				11	56.6
IR 36/NM			5	6	2			13	61.6

NM : Nihonmasari

progenies was fertile, whereas a majority of the progenies was sterile, when the Japonica tester was used as female plants. This tendency was shown in the initial crosses as well as in the repeated crosses. From the viewpoint of genotype model (Table 3-1), when Sc^j/Sc^n was crossed as pollinator to Sc^i/Sc^i, the genotype of Sc^i/Sc^j was produced more frequently than the fertile genotype, Sc^i/Sc^n in the progeny. In contrast, when Sc^i/Sc^n was crossed as pollinator to Sc^j/Sc^j, the sterile genotype of Sc^i/Sc^j, was produced more frequently than Sc^j/Sc^n. Therefore, in the Calotoc crosses,

Table 3-3. **Pollen fertility of hybrids between tester varieties and pollen-fertile progeny plants**

Crosses	No. of plants in each fertility class									Total	Mean
	-40	-50	-60	-70	-80	-85	-90	-95	-100%		%
1982											
IR 36///IR 36/Ketan Nangka//Tohoku 127											
IR 36/A16-A1				1	1	1	1	7	7	18	91.7
IR 36/A16-B5			1	2	6		1	2	3	15	80.1
IR 36///Kochihibiki//IR 36/Ketan Nangka											
IR 36/A17-A16					2	5	5	2	7	21	89.1
IR 36/A17-A22			2	2	1	1	1	2	9	18	86.2
Nihonmasari///Nihonmasari/Calotoc//IR 36											
NM/A18-A20	1	4	6	4	1		2	3	1	22	65.5
NM/A18-B3		1	1	6	2	2	2	2	6	22	79.3
Nihonmasari///IR 36//Nihonmasari/Calotoc											
NM/A19-A5	2	7	3	4	1	2	1		2	22	60.1
NM/A19-A18	3	2	4	1				1	1	12	53.8
1983											
Akihikari////IR 36///IR 36/Ketan Nangka//Tohoku 127											
Akihikari/J21a-1		3	1	2	2			5	5	18	79.8
Akihikari/J21a-10	1		4		2	1		3	2	13	73.7
Akihikari/J22a-19		1	1	2	2	1	1	3	3	14	80.0
Akihikari////IR 36///Kochihibiki//IR 36/Ketan Nangka											
Akihikari/J24-11	4		3	4	1	3	1	2	6	24	72.7
IR 36////Nihonmasari///Nihonmasari/Calotoc//IR 36											
IR 36/J25-9						3	4	6	8	21	91.5
IR 36/J26-11					2	2	2	4	12	22	92.9
IR 36////Nihonmasari///IR 36//Nihonmasari/Calotoc											
IR 36/J27-22				1		1	1	9	10	22	93.2

NM : Nihonmasari

there seemed to be an allelic interaction: A portion of Sc^n-pollen is likely to be aborted in the genotype of Sc^i/Sc^n; and Sc^j-pollen in the genotype of Sc^j/Sc^n, although the aborted gametes are morphologically not different from viable one. Superficially, the decreased number of the gametes carrying one of the alleles can be linked with a gametophyte gene. In the present study, there seems to be no need to postulate any gametophyte genes.

Testing of marker genes for duplicate lethals or gametophyte genes. Some tester lines which carry the marker genes for gametophyte genes were included in the following tests. Preliminary tests of F_1 sterility of hybrids between these additional testers and those already used indicated that the testers with the marker gene, i.e. *lg*, *bc* or *dl*, behave as ordinary Japonica testers (Table 3-4). Of these testers the *lg*-tester was used in the other tests. And *bc* and *dl* testers were used in backcross experiments to test the segregation ratio of the markers, as shown in the Table 3-5.

Table 3-4. Fertility of F$_1$s between marker lines and tester varieties

Tester varieties	Kamairazu		Muyohzetsutou		Tareba	
	Pollen %	Spikelet %	Pollen %	Spikelet %	Pollen %	Spikelet %
IR 50	48.3	27.6	47.4	27.7	48.6	28.6
Ketan Nangka	98.7	78.7	84.1	76.5	90.6	91.3
Achar Bhog	86.4	67.8	73.3	69.9	79.5	74.1
Calotoc	93.4	88.7	88.0	90.6		
Penuh Baru II	68.5	38.9	55.9	49.3		

Testers were used as pollinators.

Table 3-5. Pollen and spikelet fertility in the backcrosses of Indica-Japonica crosses

Crosses	Genotypes	No. of plants	Spikelet fertility %	Pollen fertility %
Kamairazu/IR 50//Kamairazu	*alk*/+	43	46.4	51.5)*
	alk/*alk*	15	48.5	38.4
	Ph/Ph^{+}	25	55.7)**	54.9
	Ph^{+}/Ph^{+}	33	40.4	43.3
	bc/*bc*	33	42.5)*	48.3
	bc/+	25	52.9	48.5
Tareba/IR 50//Tareba	*alk*/+	49	41.8	51.8
	alk/*alk*	5	48.2	40.5
	Ph/Ph^{+}	31	42.3	47.9
	Ph^{+}/Ph^{+}	24	41.5	53.3
	dl/+	32	43.2	47.0
	dl/*dl*	23	40.3	59.9
Kamairazu//Kamairazu/IR 50	*alk*/*alk*	22	46.2	37.0
	alk/+	30	46.1	38.1
	Ph/Ph^{+}	20	53.8	36.5
	Ph^{+}/Ph^{+}	32	45.7	38.4
	bc/+	43	51.8	39.0
	bc/*bc*	9	34.7	31.3
Kamairazu/IR 50//IR 50	*alk*/+	26	74.9)*	84.4
	+/+	38	79.9	84.6
	bc/+	27	72.1)**	81.7
	+/+	37	82.1	86.7

*, ** : Significant at 0.05% and 0.01%, respectively.

As a result, no marker genotype was directly related to pollen fertility except in one case of *alk/alk versus alk/+* in Kamairazu/IR50//Kamairazu, while some other marker genotypes were related to spikelet fertility (Table 3-5). The decrease of the proportion of the genotype *alk/alk* against *alk/+* in these crosses can be related to female gamete abortion associated with the *S-5* locus. Significant decrease of the number of male gametes carrying *bc* was confirmed when the F_1 hybrids were used as pollinators.

Relation of the fertility and genotypes was further analyzed (Table 3-6 and 3-7). In terms of spikelet fertility, a genic effect for fertility was found to be related to *Ph* from IR 50. A similar effect was observed also in the three-variety cross with Ketan Nangka (Table 2-4). The fact that the Ph/Ph^+ genotype indicated a higher fertility than the Ph^+/Ph^+ suggests that a gene near this marker has a mitigating effect on the sterility.

The level of spikelet fertility was differentiated also by some marker genotypes in the cross of Kamairazu/IR 50//IR 50. The double recessive genotype of *alk/+*, *bc/+* was significantly related to the lowest fertility. However, the genotype of *bc/+* was related to a higher spikelet fertility than the genotype of *bc/bc* in other crosses. Generally, the absence of *bc* was related to a higher fertility, as it was shown in the comparison of +/+ with *bc/+*. Therefore, the dominant allele for *bc* seems to be related to a sterility-

Table 3-6. Distribution of spikelet fertility in the backcrossed Indica-Javanica crosses (1984)

Genotype	No. of plants in each fertility class									Total	Mean	
	-20	-30	-40	-50	-60	-70	-80	-90	-100 %		%	
					Kamairazu/IR 50//Kamairazu							
Ph/Ph^+, *bc/bc*			7	2	2	1		1		13	46.8	
Ph^+/Ph^+, *bc/bc*	4	5	2	3	2	1	1	2		20	39.7	
Ph/Ph^+, *bc/+*			1	2	1	4	1	1	2	12	65.3	)*
Ph^+/Ph^+, *bc/+*	2	2	3	2	1	2	1			13	41.5	
Ph/Ph^+, *alk/alk*			2	1		1			2	6	62.5	
Ph^+/Ph^+, *alk/alk*	1	3	2		1	1		1		9	48.5	
Ph/Ph^+, *alk/+*			6	3	3	4	1	2		19	53.5	
Ph^+/Ph^+, *alk/+*	5	4	3	5	2	2	2	1		24	40.8	
					Kamairazu//Kamairazu/IR 50							
Ph/Ph^+, *bc/bc*		1			2					3	42.5	
Ph^+/Ph^+, *bc/bc*	3		1	1	1					6	30.8	
Ph/Ph^+, *bc/+*	2	1		3	3	4	3		1	17	55.8	
Ph^+/Ph^+, *bc/+*	2	2	1	7	9	2	2	1		26	49.2	
Ph/Ph^+, *alk/alk*	1				3	2	2		1	9	61.4	
Ph^+/Ph^+, *alk/alk*	3	1		2	4	1	1	1		13	46.4	
Ph/Ph^+, *alk/+*	1	2		3	2	2	1			11	47.6	
Ph^+/Ph^+, *alk/+*	2	1	2	6	6	1	1			19	45.3	
					Kamairazu/IR 50//IR 50							
+/+, *bc/+*					2	2	6	4	1	15	75.6	)**
***alk*/+, *bc*/+**				1	1	4	6			12	67.7	)*
+/+, +/+						2	6	7	7	23	82.7	)**
alk/+, +/+						1	4	6	3	14	81.2	
					IR 50//Kamairazu/IR 50							
bc/+								1		1	84.1	
+/+						4	7	4		15	74.7	

*, ** : Significant at 0.05% and 0.01%, respectively.

Table 3-7. **Distribution of pollen fertility in the backcrossed Indica-Javanica crosses (1984)**

Genotype	No. of plants in each fertility class										Total	Mean	
	-10	-20	-30	-40	-50	-60	-70	-80	-90	-100 %		%	
	Kamairazu/IR 50//Kamairazu												
Ph/Ph⁺, bc/bc		1	1	3	1	4		1		2	13	51.7	
Ph⁺/Ph⁺, bc/bc		3	3	3	5	2		1	1	2	20	44.4	
Ph/Ph⁺, bc/+			2	2		4		1		3	12	58.4	)*
Ph⁺/Ph⁺, bc/+		3	4			2	3	1			13	39.3	
Ph/Ph⁺, alk/alk	1		1	1		2		1			6	42.1	
Ph⁺/Ph⁺, alk/alk	1	1	3	2			1			1	9	36.0	
Ph/Ph⁺, alk/+			2	4	1	6		1		5	19	59.0	
Ph⁺/Ph⁺, alk/+		4	4	1	5	4	2	2	1	1	24	44.8	
	Kamairazu//Kamairazu/IR 50												
Ph/Ph⁺, bc/bc			2	1							3	26.9	
Ph⁺/Ph⁺, bc/bc		3	1	1							5	33.5	
Ph/Ph⁺, bc/+		2	3	6		6					17	38.2	
Ph⁺/Ph⁺, bc/+		4	2	9	3	5	2	1			26	39.5	
Ph/Ph⁺, alk/alk			2	3		4					9	41.4	
Ph⁺/Ph⁺, alk/alk		3	1	6		2	1				13	34.0	
Ph/Ph⁺, alk/+		2	3	4		2					11	32.6	
Ph⁺/Ph⁺, alk/+		4	2	4	3	3	1	1		1	19	41.4	
	Kamairazu/IR 50//IR 50												
+/+, bc/+						1	1	1	3	9	15	87.2	)*
alk/+, bc/+					2	3		1		6	12	74.8	)**
+/+, +/+						3	2	4	2	12	33	83.0	)*
alk/+, +/+								1	2	11	14	92.7	
	IR 50//Kamairazu/IR 50												
bc/+										1	1	97.9	
+/+							1	1	2	11	15	91.8	

*, ** : Significant at 0.05% and 0.01%, respectively.

mitigating effect. Throughout the crosses indicated in Table 3-5, the dosage of *Ph* and bc^+ is related to a higher level of spikelet fertility. Similar facts were observed for the pollen fertility (Table 3-7). In the cross of Kamairazu/IR 50//IR 50, two genotypes, *alk/+, bc/+* and *alk/+, +/+* showed a contrasting level of pollen fertility. It seemed that there is a sterility-mitigating gene near the bc^+ locus. The effect of *bc*-genotype-related effect was not observed in other crosses. Probably, there is some unknown locus which may affect the pollen fertility. And the decrease of the number of genotypes with *bc* and Ph^+ lowered the level of fertility and might have hindered the clear manifestation of the genic effect.

Discussion

The genetic nature of the WCV's wide-compatibility gene for the pollen fertility can be simply ascribed to an allelic interaction rather than to the two-locus model and gametophyte genes. If we apply the two-locus model to the tracing of the WCV's wide-compatibility gene, there should be at least two independent loci and a gametophyte gene near each of the two loci. But, a single locus for an allelic interaction can explain the cause of distorted segregation and sterility, as it was demonstrated by Kitamura (1962, 1963).

Iwata *et al.* (1964) reported the presence of gametophyte gene *ga* which controls the selective fertilization of gametes in the cross between an atomic-bomb-irradiated mutant and a normal variety. The F_1 hybrid showed normal spikelet fertility, but a low pollen fertility of 58.7 percent. The distorted segregation of the marker genes, *wx* and *C* was proved to be independent of the level of pollen fertility.

Nakagahra *et al.* (1972) and Nakagahra (1972) reported the presence of two gametophyte genes ga_2 and ga_3 near the loci of marker genes, *bc* and *dl*. Nakagahra *et al.* (1974) also reported the presence of gametophyte gene ga_4 in a locus near *wx, C* and *alk*. Nakagahra (1981) reported another gametophyte gene ga_8 in the third linkage group. In these cases, the relation between the distorted segregation and the level of pollen fertility was not examined, and the distorted segregation of the markers was found to be independent of the spikelet fertility. There remains the possibility that the gametophyte genes could have been related to the level of pollen fertility, since the level of pollen fertility is independent of spikelet fertility in many cases.

In the present experiment, the marker genes, *bc* and *alk* which were reported as the markers of the gametophyte genes were found to be related in some way to the fertility of pollen. Likewise, the marker gene, *Ph* was related to the level of pollen fertility.

Recently, Naekawa (1981, 1985) reported the presence of other series of gametophyte genes, i.e. ga_6 near *lg* in the linkage group II, and ga_7 and ga_9 in the linkage group III. In his experiments, F_1 hybrids between Japonica varieties were tested and their level of fertility was normal. Mori *et al.* (1973) reported that the segregation of some markers *Wx, C* and *alk* was significantly biased from the normal ratio when F_1 hybrids between distantly related varieties were crossed as pollinators. The bias was observed even when the F_1 hybrids with morphologically normal pollen fertility were chosen for their testing. They attributed the distorted segregation to a competitive fertilization among functionally normal pollen, and assumed the role of gametophyte genes, ga_A and ga_B which control the selective fertilization.

In some of these works, although distorted segregation was found despite morphologically normal pollen, there is no basis to assume that the morphologically normal appearance of pollen is an indication of the normal function of the pollen. The work by Iwata *et al.* (1964) was an exception in the fact that the distortion was shown to be independent of the level of pollen sterility. In that case, the pollen sterility might be also affected by some other loci in additon to *ga*. In the present study, the F_1 hybrids between Calotoc and Indica or Japonica testers showed a normal pollen under microscope, but significant bias from an equal chance of fertilization was observed in the ratio of pollen-fertile *versus* pollen-semi-sterile plants. Shinjo (unpublished) observed one type of cytoplasmic male sterility, in which the pollen was morphologically normal despite its lack of function.

The concept of gametophyte genes is based on the assumption that there are genes which control selective fertilization among functionally sound pollen genotypes. But, the evidence for the competitive fertilization among functionally sound pollen was rarely provided by the former workers. The distorted segregation may be better interpreted as the expression of an allelic interaction and other genetic mechanism for gamete abortion.

In relation to some loci which seem to mitigate sterility, Kitamura's (1962, 1963) analysis of a hybrid sterility draws our attention. In the crosses of Japonica varieties and some lines obtained through repeated backcrosses of the Japonica variety to an Indica variety, Tetep, a recessive sterility gene, *a* and an inhibitor for it, *I* were identified from Tetep, and the alleles, *A* and *i* were derived from the Japonica. The genotype *aa* and *Aa* gave fixed or segregating sterile plants. But, the degree of the sterility was suppressed by *II* or *Ii* in variable degrees. Progenies with genotype of *aa II* showed fixed semi-sterility. Segregation distortion of marker genes can also be caused by this kind of sterility system. The sterility-mitigating loci near *Ph* or bc^+ may be associated with the inhibitor *I*.

Summary

The effect of the WCV's wide compatibility in terms of pollen fertility was traced through three-variety crosses and several steps of repeated hybridization.

In the Ketan Nangka crosses, the ratio of pollen-fertile plants was not different between the two-crosses, i.e. IR 36/Ketan Nangka//Japonica variety and Japonica variety//IR 36/Ketan Nangka. In the Calotoc crosses, the cross of IR 36/Calotoc//Japonica variety segregated a larger number of fertile plants than its reciprocal, Japonica variety//IR36/Calotoc.

In the further tests, those pollen-fertile plants from the Indica/Ketan Nangka//Japonica cross were crossed to the Indica tester (IR 36) as pollinator. Likewise, the pollen-fertile plants from the cross of IR 36//Japonica/Calotoc were crossed to the Japonica tester (Nihonmasari) as pollinator. Out of the progeny of these crosses, the pollen-fertile plants were further crossed to the respective tester as pollinator.

The segregation of a certain number of fertile plants after each of the successive croses was assumed to be the evidence that the WCVs have such a gene as Sc^n for pollen fertility and Indica and Japonica testers possess Sc^i and Sc^j, respectively, as reported by Kitamura (1962, 1963).

The ratio of fertile *versus* semi-sterile plants was nearly 1:1 in the Ketan Nangka crosses. In the Calotoc crosses, when the cross was in the format of $Sc^i//Sc^n/Sc^j$, the majority of the progenies was fertile, whereas a majority of the progenies was sterile, when the cross was in the format of $Sc^j//Sc^n/Sc^i$. Therefore, in the Calotoc crosses, there seemed to be an allelic interaction: A portion of S^n-pollen is likely to be aborted in the genotype of Sc^i/Sc^n; and a portion of Sc^j pollen in the genotype of Sc^j/Sc^n. It was concluded that the combination of two of the Sc^i, Sc^j and Sc^n alleles can be the basis for the allelic interaction through which gamate abortion was caused and measured by the ratio of semi-sterile plants.

In a further experiment, Japonica testers with additonal marker genes, i.e. *bc* (brittle culm) and *lop-2* (dl-lopped leaf -2) of the XIth linkage group were tested in addition to *alk*, C^+, Ph^+ and so on. Some experimental Japonica lines with these markers were crossed to Indica testers in backcrossing experiments, and the relation between these markers and pollen or spikelet fertility was examined.

In terms of the spikelet fertility, a genic effect for the fertility was found to be related to *Ph* from IR 50. The fact that the Ph/Ph^+ genotype indicated a higher fertility than the Ph^+/ph^+ suggests that a gene near this marker has a mitigating effect on the sterility.

The level of pollen fertility was differentiated also by some marker genotypes in the cross of Kamairazu/IR 50//IR 50. The double recessive genotype of *alk*/+, *bc*/+ was significantly related to the lowest fertility. However, the genotype of *bc*/+ was related to a higher pollen fertility than the genotype of *bc/bc* in other crosses. Generally, the decrease of the dosage of *bc* was related to a higher fertility. The concurrent effect of the dosage of *Ph* and bc^+ is related to the higher level of the pollen fertility. Significant decrease of the number of male gametes carrying *bc* was confirmed when the F_1 hybrids were used as pollinators. It seemed that there is a pollen-sterility-mitigating gene near the bc^+ locus. Further analyses are necessary for determining the genetic function of these loci.

IV. Genetic analyses of F_1 sterility of hybrids between Aus varieties and Indica, Japonica or Javanica varieties

In the preceding parts, it was indicated that Aus varieties include various compatibility types in terms of F_1 sterility with Indica and Japonica testers, and that the types of the compatibility are likely to be different from those of other groups. Therefore, the same methods as those applied to the analysis of Indica-Japonica hybrids were attempted for the crosses between Aus varieties and the other types. One limitation for the analyses with Aus varieties was that no WCV type was found in the initial experiment, although some WCV types were identified later.

Materials and Methods

In the analyses of Aus varieties, the WCVs used in the previous tests were not effective for Aus varieties, although a variety, Dular was later found to be widely compatible with most of the Indica, Japonica and Javanica varieties. Therefore, according to the format of crosses used in the gamete elimination analyses, backcrosses of Japonica/Aus varieties//Japonica were made, and in the B_1F_1, the relation between the level of the fertility and the marker gene was analyzed. Similarly, Aus varieties or WCV were backcrossed, and the relation between the level of fertility and marker genes was tested with B_1F_1.

In the following tests, the Japonica varieties with the marker genes, *bc* or *dl* in the linkage group XI were added. The compatibility of these varieties was shown to be of the Japonica type (Table 3-4). Out of the Aus varieties, those showing sterility both with Indica and Japonica varieties were chosen for the crosses.

Results

Analyses of hybrid sterility between Aus varieties and Japonica varieties. In the five crosses of this type, the frequency of marker genes was determined, as shown in Tables 4-1 and 4-2. The frequency of some marker genes was found to be significantly different from the normally expected ratio of 1:1. For example, the ratio of alk:alk^+ was apparently different from 1:1 in the cross of Taichung 65//Taichung 65/Panbira, and the frequency of *alk* and A^+ was reduced significantly (Table 4-1). Likewise, the frequency of Ps^+ and *dl* was extremely reduced in the cross of Tareba/Achar Bhog (Table 4-2). The frequency of gametes jointly carrying these markers was reduced remarkably (Table 4-2).

The reduced frequency of some markers was expected to be related to the fertility of spikelet or pollen, however, no significant difference in the fertility levels was observed between the different marker genotypes except for a few cases (Table 4-3 and 4-4).

In the cross of Taichung 65//Taichung 65/Panbira, it was possible to relate the level of fertility to the marker genotypes (Table 4-5). In terms of pollen fertility, the genotype of A/A^+, alk/alk showed the lowest level of pollen fertility, and the genotype of A^+/A^+, alk/alk^+ showed only a few of individual plants with low fertility. Therefore, it is likely that there are two independent loci which affect the level of pollen fertility. The sterility seems to be related to the genotype of A/A^+, but suppressed by a genic

Table 4-1. Frequency of genotypes in Aus-Japonica crosses I

Crosses	Genotypes & Frequency				Probability (equal ratio)
	A/A^+	A^+/A^+			
T65//T65/Panbira	27	39			0.2 — 0.1
T65/DZ151//T65	27	43			0.1 — 0.05
AK/Achar Bhog//TM	12	28			0.02 — 0.01
	alk/+	*alk/alk*			
T65//T65/Panbira	42	24			0.05 — 0.02
T65/DZ151//T65	38	32			0.5 — 0.3
AK/Achar Bhog//TM	23	15			0.2 — 0.1
	A/A^+ *alk/+*	A^+/A^+ *alk/+*	A/A^+ *alk/alk*	A^+/A^+ *alk/alk*	
T65//T65/Panbira	17	25	10	14	0.1 — 0.05
T65/DZ151//T65	15	23	12	20	0.3 — 0.2
AK/Achar Bhog//TM	6	17	5	10	0.05 —.02

T65, AK and TM denote Taichung 65, Akihikari and Tatsumi-mochi, respectively.

Table 4-2. Frequency of genotypes in Aus-Japonica crosses II

Genotypes				Ratio				Probability (equal ratio)
Tareba (*dl*)/Achar Bhog//Tareba								
	alk/+	*alk/alk*			27	21		0.5—0.3
	Ps/Ps^+	Ps^+/Ps^+			31	17		0.05—0.02
	dl/+	*dl/dl*			32	16		0.05—0.02
alk/+ *dl/dl*	*alk/+* *dl/+*	*alk/alk* *dl/dl*	*alk/alk* *dl/+*	9	18	7	14	0.2—0.1
alk/+ Ps/Ps^+	*alk/+* Ps^+/Ps^+	*alk/alk* Ps/Ps^+	*alk/alk* Ps^+Ps^+	16	11	15	6	0.2—0.1
dl/+ Ps/Ps^+	*dl/+* Ps^+/Ps^+	*dl/dl* Ps/Ps^+	*dl/dl* Ps^+/Ps^+	22	10	9	7	$p<0.01$
Muyohzetsu-tou/Achar Bhog//Muyohzetsu-tou								
	alk/+	*alk/alk*			31	45		0.2—0.1
	Ps/Ps^+	Ps^+/Ps^+			39	37		0.9—0.8
	lg/+	*lg/lg*			40	36		0.7—0.5
alk/+ Ps/Ps^+	*alk/+* Ps^+/Ps^+	*alk/alk* Ps/Ps^+	*alk/alk* Ps^+/Ps^+	11	20	28	17	0.05—0.01
alk/+ *lg/+*	*alk/+* *lg/lg*	*alk/alk* *lg/+*	*alk/alk* *lg/lg*	14	17	22	23	0.5—0.3

Table 4-3. Distribution of spikelet fertility in Aus-Japonica crosses

Marker genotype	No. of plants in each fertility class								Total	Mean %	t-test
	-30	-40	-50	-60	-70	-80	-90	-100 %			
Taichung 65//Taichung 65/Panbira											
alk/+	1		3	2	7	7	10	12	42	77.6	
alk/alk	2	1	3		2	4	6	6	24	72.5	
A/A^{+}	3		4		3	2	6	9	27	72.6	
A^{+}/A^{+}		1	2	2	6	9	10	9	39	77.9	
Akihikari/Achar Bhog//Tatsumi-mochi											
alk/+		1		1	2	4	4	11	23	83.9	
alk/alk	1		2			3	4	5	15	77.6	
A/A^{+}		1		1	2	2	2	3	11	76.0	
A^{+}/A^{+}	1		2			5	6	13	27	84.1	
Taichung 65/DZ151//Taichung 65											
alk/+				2	3	11	14	8	38	81.6	
alk/alk					3	7	12	10	32	84.6	
A/A^{+}					2	7	14	4	27	82.9	
A^{+}/A^{+}				2	4	11	12	14	43	82.8	
Tareba/Achar Bhog//Tareba											
alk/+		1	1	3	3	4	7	8	27	77.7	
alk/alk			1	4	1	2	10	3	21	76.5	
Ps/Ps^{+}			1	4	3	2	12	9	31	85.9	*
Ps^{+}/Ps^{+}		1	1	3	1	4	5	2	17	71.7	
dl/+			2	3	2	3	12	10	32	81.0	*
dl/dl		1		4	2	3	5	1	16	69.0	
Muyozetsu-tou/Achar Bhog//Muyozetsu-tou											
alk/+					1	6	12	12	31	86.7	
alk/alk		1			3	6	18	17	45	84.9	
Ps/Ps^{+}					2	5	13	19	39	86.9	
Ps^{+}/Ps^{+}		1			2	7	17	10	37	84.3	
lg/+					1	3	13	19	36	89.0	
lg/lg		1			3	8	17	11	40	83.1	

* : Significant at 0.05%.

Table 4-4. Distribution of pollen fertility in Aus-Japonica crosses

Marker genotype	No. of plants in each fertility class -20	-30	-40	-50	-60	-70	-80	-90	-100 %	Total	Mean %	t-test
Taichung 65//Taichung 65/Panbira												
alk/+				1		2	7	10	22	42	86.8	
alk/*alk*			1	1	1	5	4	3	9	24	79.1	
A/A^{+}			1	1	1	6	6	6	6	27	75.9	**
A^{+}/A^{+}				1		1	5	7	25	39	89.6	
Akihikari/Achar Bhog//Tatsumi-mochi												
alk/+				1	3	4	4	5	6	23	76.5	
alk/*alk*	1				3	2	1	1	7	15	76.0	
A/A^{+}					2	4	2	1	2	11	73.1	
A^{+}/A^{+}	1			1	4	2	3	5	11	27	77.6	
Taichung 65/DZ151//Taichung 65												
alk/+			2	3		8	2	5	18	38	80.3	
alk/*alk*			1	2	1	2	3	3	20	32	84.9	
A/A^{+}				4	1	5	3	2	12	27	79.2	
A^{+}/A^{+}			3	1		5	2	6	26	43	84.4	
Tareba (*dl*)/Achar Bhog//Tareba (*dl*)												
alk/+	1			2	6	4	3	5	6	27	72.1	
alk/*alk*	2		2	1	1	4	2	4	5	21	67.3	
Ps/Ps^{+}	3			2	3	6	3	6	8	31	70.9	
Ps^{+}/Ps^{+}			2	1	4	2	2	3	3	17	72.4	
dl/+				2	1	3	2	4	4	16	76.2	
dl/*dl*	3		2	1	6	5	3	5	7	32	66.9	
Muyozetsu-tou (*lg*)/Achar Bhog//Muyozetsu-tou (*lg*)												
alk/+	1		2		2	2	9	6	9	31	76.9	
alk/*alk*		1		2	2	8	11	9	12	45	77.1	
Ps/Ps^{+}	1		1	2	1	5	8	10	11	39	77.0	
Ps^{+}/Ps^{+}		1	1		3	5	12	5	10	37	77.1	
lg/+			2	2	1	5	10	9	7	36	75.5	
lg/*lg*	1	1			3	5	10	6	14	40	78.4	

*, ** : Significant at 0.05% and 0.01%, respectively.

Table 4-5. Distribution of pollen and spikelet fertility in the cross of Taichung 65//Taichung 65/Panbira, B_1F_1

Marker genotypes	No. of plants in each fertility class -30	-40	-50	-60	-70	-80	-90	-100 %	Total	Mean %
					Pollen fertility					
A/A^{+}, *alk/alk*		1		1	4	3		1	10	66.6
A^{+}/A^{+}, *alk/alk*			1		1	1	3	8	14	88.0 **
A/A^{+}, *alk/+*			1		2	3	6	5	17	81.3 *
A^{+}/A^{+}, *alk/+*						4	4	17	25	90.5 **
					Spikelet fertility					
A/A^{+}, *alk/alk*	2		3		1	1		3	10	61.1
A^{+}/A^{+}, *alk/alk*		1			1	3	6	3	14	80.6 *
A/A^{+}, *alk/+*	1		1		2	1	6	6	17	79.4 *
A^{+}/A^{+}, *alk/+*			2	2	5	6	4	6	25	76.3

*, ** : Significant at 0.05% and 0.01%, respectively.

effect related to alk^{+} from Panbira. The locus near A for the allelic interaction can be tentatively named *S-6*. A similar, but a slightly less significant relationship between the genotypes and the level of sterility was found in the spikelet fertility.

Analyses of hybrid sterility including WCVs and Aus varieties. Initially, Aus 373 seemed to be a WCV, and was included in the paired crosses along with the other WCVs. The results are presented in Table 4-6. Spikelet fertility in the cross of Aus 373/IR 50//Akihikari was related to the genotype of C/C^{+}, suggesting that an allelic interaction between an allele from IR 50 and another from Akihikari was responsible for the spikelet sterility. Therefore, the already known effect of $S\text{-}5^{i}/S\text{-}5^{j}$ can be indicated in this case, although this effect alone cannot explain the distribution of the spikelet sterility. The pollen fertility in the cross of Aus 373/Akihikari//IR 50 was found to be weakly related to the C/C^{+} genotype. This fact may indicate that an allelic interaction between an allele from Aus 373 and another from IR 50 lowered the pollen fertility, suggesting that the allelic interaction between this Aus variety and IR 50 is stronger than that between IR 50 and Akihikari.

In additional tests, five crosses were tested, in which Ketan Nangka was added to the cross between the Aus variety and an Indica or a Japonica variety, but no clear relationship between the fertility level and the marker genotypes was found.

Probably, there may have been various kinds of allelic interaction in these crosses of different varietal groups, and the expression of the sterility may be complicated. Another possibility is that such interactions may not be detected with the limited number of marker genotypes.

After the three way crosses, described above, a different kind of three way crosses was tested, in which one Aus variety and two WCVs were crossed to detect the allelic interaction between the Aus varieties and the Javanica WCVs. An Aus variety with red pericarp, Ingra was used in the Ingra/Ketan Nangka//CPSLO 17, where the cross between Ketan Nangka and CPSLO 17 did not show hybrid sterility, and the sterility could only be traced to Ingra and CPSLO 17. In this cross, the level of spikelet fertility was soley related to the *Rc* locus in the linkage group IV (Table 4-7). Therefore, one of the bases for the pronounced hybrid sterility between Javanica varieties and Aus varieties can be attributed to an allelic interaction at the locus near the *Rc*, and can be designated as *S-7*.

Table 4-6. Distribution of pollen and spikelet fertility in the three way crosses with Aus 373, IR 50 and Akihikari

Marker gene	No. of plants in each fertility class									Total	Mean	t-
	-20	-30	-40	-50	-60	-70	-80	-90	-100 %		%	test
Pollen fertility												
Aus 373/IR 50//Akihikari												
C/C^+	1	2	12	4	4	2	1	3	4	33	52.6	
C^+/C^+	1	2	5	4	2	2	4	4	2	26	57.9	
Ph/Ph^+		2	7	3	2	1	2	4	3	24	58.4	
Ph^+/Ph^+	2	2	10	5	3	4	3	3	3	35	52.6	
Ph/Ph^+, C/C^+		1	7	1	1			1	2	13	50.8	
Ph/Ph^+, C^+/C^+		1		2	1	1	2	3	1	11	67.3	
Ph^+/Ph^+, C/C^+	1	1	5	3	3	2	1	2	2	20	53.9	
Ph^+/Ph^+, C^+/C^+	1	1	5	2	1	1	2	1	1	15	51.0	
Aus 373/Akihikari//IR 50												
C/C^+	1	2	5	4	5	5	1		1	24	49.9	*
C^+/C^+			3	5	8	2	1	2	4	25	61.2	
+/+	1	2	5	6	5	4	1	1	2	27	51.8	
alk/+			3	3	8	3	1	1	3	22	60.4	
Spikelet fertility												
Aus 373/IR 50//Akihikari												
C/C^+		1	3	8	6	9	4	2		33	57.5	**
C^+/C^+	1	2	7	5	3	7	1			26	47.4	
Ph/Ph^+	1	1	4	8	2	5	2	1		24	52.0	
Ph^+/Ph^+		2	6	6	6	11	3	1		35	53.8	
Ph/Ph^+, C/C^+			2	6	2	1	1	1		13	54.6	
Ph/Ph^+, C^+/C^+	1	1	2	1	1	4	1			11	49.0	
Ph^+/Ph^+, C/C^+		1	1	2	4	8	3	1		20	59.5	**
Ph^+/Ph^+, C^+/C^+		1	5	4	2	3				15	46.3	
Aus 373/Akihikari//IR 50												
C/C^+	1	3	5	5	3	3	4			24	47.3	
C^+/C^+	2	4	8	5	3	3				25	40.6	
+/+	1	5	5	7	2	3	4			27	45.3	
alk/+	2	2	8	3	4	3				22	42.2	

Note : The recombination value between *C* and *alk* in the cross of Aus 373/Akihikari was evaluated at 0.143.
*, ** : Significant at 0.05% and 0.01%, respectively.

Table 4-7. **Distribution of pollen and spikelet fertility in the cross of Ingra/Ketan Nangka//CPSLO 17**

Genotype	No. of plants in each fertility class								Total	Mean	
	-30	-40	-50	-60	-70	-80	-90	-100 %		%	
				Spikelet fertility							
wx/wx		2	3	10	3	5	12	11	46	73.8	
wx/+		2	9	9	5	1	14	12	52	71.8	
Ph/Ph^+		3	4	9	5	3	14	8	47	70.8	
Ph^+/Ph^+		1	7	10	3	2	12	16	51	74.9	
Rc/Rc^+		3	11	14	5	2	2	1	38	55.9	**
Rc^+/Rc^+		1	1	5	3	3	19	28	60	83.7	
				Pollen fertility							
wx/wx				3	2	9	13	19	46	84.7	
wx/+				1	1	7	15	28	52	88.2	
Ph/Ph^+				2	1	8	14	22	47	86.6	
Ph^+/Ph^+				2	2	8	14	25	51	86.5	
Rc/Rc^+				1	2	3	17	15	38	86.5	
Rc^+/Rc^+				3	1	13	11	32	60	86.6	

** : Significant at 0.01%.

Table 4-8. **Distribution of pollen and spikelet fertility in the crosses between Aus varieties and Indicas**

Marker genotypes	No. of plants in each fertility class							Total	Mean
	-40	-50	-60	-70	-80	-90	-100 %		%
				Pollen fertility					
				Achar Bhog//Achar Bhog/IR 36					
Ph/Ph^+				2		1	28	31	93.8
Ph^+/Ph^+					4	4	23	31	91.4
				IR 36/DZ 151//IR 36					
C/C^+						3	46	49	95.9
C^+/C^+						6	41	47	94.8
				Spikelet fertility					
				Achar Bhog//Achar Bhog/IR 36					
Ph/Ph^+				1	2	3	25	31	90.8
Ph^+/Ph^+					1	4	26	31	92.6
				IR 36/DZ 151//IR 36					
C/C^+					4	10	35	49	91.2
C^+/C^+				2	2	17	26	47	89.3

Crosses with Aus varieties and IR varieties. Some additional tests with backcrosses of Indica or Aus variety were carried out, but the resulting levels of fertility was generally high, and no linkage relationship was suggested (Table 4-8). In the previous section, where the cross between Aus varieties and Japonica testers was backcrossed by Japonica testers, a remarkably low level of fertility was observed, and some linkage relationships between the level of fertility and the markers were found. Contrastingly, when the Indica tester was backcrossed, the fertility was not lowered. The IR varieties may have some suppressor genes for some allelic interaction for the sterility.

Discussion

The hybrid sterility between Indica and Japonica or between Indica and Javanica varieties was able to be related to an allelic interaction at the particular locus, *S-5*. This finding was confirmed with the use of WCVs which have a set of suitable marker genes. In the analyses of the hybrid sterility between Aus varieties and other groups of varieties, the methods which were effective for the analysis of Indica-Japonica or Indica-Javanica crosses were not applicable, since the WCVs produce sterility in their crosses to Aus varieties. As the Aus group has diverse compatibility types, it was necessary to backcross an Indica or Japonica variety to the original single crosses between an Aus variety and one of the other varieties.

There was another methodological limitation. Some marker genes from the linkage groups I, II, III, IV and XI were available, but those from other linkage groups were not. According to Sano *et al.* (1979), an allelic interaction at a locus near *la* in the linkage group VIII was responsible for the hybrid sterility in the interspecific hybrid between *Oryza glaberrima* and *O. sativa.* It is likely that some additional loci in the linkage groups from V to X, and XII may be related to the sterility. Due to these difficulties, only a few cases of clear indication of allelic interaction were found despite the large number of crosses tested.

A case of pollen sterility was related to the genotype of A/A^+, and a suppressing genic effect was related to the alk^+ from Panbira in the cross of Taichung 65//Taichung 65/Panbira. If the two-locus model is applicable to this case, the sterility must be lowest in the double-heterozygous genotype of A/A^+, *alk*/+, but in actually data, the sterility was lowest in the genotype of A/A^+, *alk/alk*. The sterility can be related primarily to a heterozygous locus near the marker *A* (Anthocyanin activator) in the linkage group III. Kitamura (1962, 1963) identified a sterility-causing gene, *a* and an inhibitor to it, *I* in an Indian variety, Tetep. The *a* and *I* genes seem to correspond to the genic effect related to A/A^+ and alk^+, respectively. Further tests are necessary to confirm the allelic interaction at the *S-6* locus.

With hybrids between Japonica varieties, gametophyte genes, ga^7 and ga^9 were reported near the *A* locus (Maekawa, 1981). Another gametophyte gene, ga^8 was reported in the same linkage group III to cause a segregation distrotion in the hybrids of distantly related varieties (Nakagahra, 1981). So far, such a gametophyte gene has never been related to pollen sterility, as there was no test of the relation between the gametophyte gene and the level of pollen sterility. In some cases, segregation distortion was found when a F_1 was used as pollen donor which shows no indication of pollen sterility (Mori *et al.*, 1973; Naekawa *et al.,* 1981, 1985). However, microscopic observation may not be adequate to test pollen function, as some cases were reported in which the pollen function was lost despite the normal morphological appearance of pollen (Shinjo, unpublished). Contrary to the previous view that competitive fertilization of pollen is affected by the gametophyte genes, the presents result suggest that the sterility-causing allelic interaction and such genes as those suppressing the allelic interaction may be the basis for the segregation distrotion. Gamete elimination may also be caused by the *a* and *I* system of sterility (Kitamura, 1962, 1963).

Another important fact found in the cross of Ingra/Ketan Nangka//CPSLO 17 is that the hybrid sterility between WCV and Aus varieties is caused by an allelic interaction at a particular locus, *S-7* which seemed to be located very near to the *Rc* (Red pericap) locus. It is highly probable that a set of multiple alleles can be found at this locus. Through the differentiation of the alleles at the *S-7* locus, varietal difference of compatibility between the Aus group and the rest of the varietal groups can be explained, in the same way that the spikelet sterility in the crosses among Indica, Japonica and Javanica varieties was ascribed to the allelic interaction of multiple alleles at the *S-5* locus.

Summary

In the genetic analyses of the compatibility of Aus varieties, backcrosses of Japonica/Aus varieties//Japonica were made, and in other cases, Aus varieties or WCV were backcrossed. In the B_1F_1, the relation between the level of fertility and the marker gene was analyzed. Out of the Aus varieties, those showing F_1 sterility when crossed to Indica and Japonica varieties were chosen for the crosses.

In the cross of Taichung 65 (Japonica)//Taichung 65/Panbira, the genotype of A/A^+ alk/alk showed the lowest level of pollen fertility, and the genotype of A/A^+ $alk/+$ showed only few low-fertility plants. Therefore, the pollen sterility seemed to be related to the genotype of A/A^+, but suppressed by a genic effect related to alk^+ from Panbira. This locus near *A* for the allelic interaction is tentatively designated as *S-6*. A similar, but a slightly less significant relationship was found between the genotypes and the level of spikelet sterility. Likewise, the frequency of Ps^+ and *dl* was extremely reduced in the cross of Tareba (Japonica)/Achar Bhog. The frequency of gametes jointely carrying these markers was remarkably reduced.

An Aus variety, Aus 373 initially seemed to be a WCV. The spikelet fertility in the cross of Aus 373/IR 50//Akihikari was related to the genotype of C/C^+, suggesting an allelic interaction of $S\text{-}5^i/S\text{-}5^j$ and the linkage $S\text{-}5^n$ and *C* in Aus 373. The pollen fertility in the cross of Aus 373/Akihikari//IR 50 was weakly related to the C/C^+ genotype, suggesting that the allelic interaction between this Aus variety and IR 50 is stronger than that between IR 50 and akihikari.

A clear case of allelic interaction was found, when an Aus variety with red pericarp, Ingra was used in the Ingra/Ketan Nangka//CPSLO 17 cross. The cross between Ketan Nangka and CPSLO 17 did not show hybrid sterility, and the sterility could only be traced to the combination of Ingra and CPSLO 17. In this cross, the level of spikelet fertility was solely related to *Rc* locus in the linkage group IV. Therefore, one of the bases for the pronounced hybrid sterility between Javanica varieties and Aus varieties can be attributed to an allelic interaction at this locus. Which is tentatively designated as *S-7*.

Some additional tests with backcross of Indica or Aus variety were carried out. When the Indica tester was backcrossed, the fertility was not lowered. The IR varieties may have some suppressor genes for some allelic interaction for sterility.

V. Effect of F_1 sterility on the successive generations

In the preceding parts, the genetic nature of F_1 sterility was clarified, and attributed to the allelic interaction at one locus. However, the whole features of hybrid sterility must be far more complex than those caused by some allelic interaction. One of the facts that cannot be explained by the allelic interaction is the sterility fixed in homogeneous status in later generations (Kitamura, 1962, 1963; Oka and Doida, 1962; Yokoo, 1984). There are presumably other types of sterility which may be caused by chromosomal aberrations associated with distant crosses. The extent to which the allelic interaction affects the sterility in later generations is also not well understood, because a valid theoretical model was not available in the previous studies.

The primary objectives here are to clarify the genetic analysis of the F_1 sterility, however, some of the patterns of the sterility in later generations were described with small sample populations.

Materials and Methods

Several experiments were independently carried out.

Firstly, a small number of semi-sterile individual plants in the F_2 population were chosen to determine whether the sterility is fixed or not in successive generations. For this experiment, a cross between an Indica tester, IR 36 and a Japonica tester, Nihonmasari was examined. In each of the F_2 populations of IR 36/Nihonmasari and Nihonmasari/IR 36, five plants each with normal fertility or semi-sterility were chosen, and the level of sterility was recorded in the F_3 generation. From F_4 to F_5, some selected lines with semi-sterility were checked for their segregation.

Secondly, in some Javanica varieties, the distribution of sterility in the F_2 generation of Javanica-Indica and Javanica-Japonica crosses was compared to study the relationship between the level of F_1 sterility and that in the F_2 generation.

Thirdly, a few plants were selected in the F_2 of the crosses, Indica/WCV and Japonica/WCV, and some lines were tested to study the nature of the semi-sterility found in the cross of WCVs.

Lastly, the effect of the $S\text{-}5^n$ allele incorporated into a Japonica background was examined. This is actually a part of the breeding program to utilize the $S\text{-}5^n$ gene for widely compatible lines. Since the $S\text{-}5^n$ gene is closely linked with the C^+ gene, which controls the apiculus pigmentation, if any plants with the apiculus pigmentation in the progeny of WCV/Japonica or Indica are selected, it may be easy to select lines which carry the $S\text{-}5^n$ gene. One of the experimental lines which were developed by this procedure was crossed to an Indica tester as well as to some other varieties to detect the effect of the $S\text{-}5^n$ gene.

Results

Semi-sterile progeny in Indica-Japonica crosses. In 1980, 69 plants and 91 plants, respectively, in the F_2 of IR 36/Nihonmasari and Nihonmasari/IR 36 were studied for their spikelet fertility (Table 5-1). Out of them, five each of fertile and semi-sterile plants were chosen, and approximately 20 progeny plants from each of the F_2 plants were grown as F_3 lines. The distribution of the fertility in each of the F_3 lines is shown in Table 5-2. A few plants with a low fertility were found in the

Table 5-1. Distribution of spikelet fertility of tester varieties and their hybrids

Varieties or their hybrids	No. of plants in each fertility class								Total	Mean
	-30	-40	-50	-60	-70	-80	-90	-100 %		%
				Tests at Tsukuba in 1980						
Calotoc							8	2	10	87.7
Nihonmasari (NM)								10	10	97.0
Ketan Nangka (KN)						1	4	5	10	89.1
F_2 NM/KN				2		8	31	35	76	88.2
F_1 NM/KN							2	8	10	87.7
IR 36							5	5	10	90.2
F_2 IR 36/NM	12	5	11	4	10	10	11	6	69	59.4
F_1 IR 36/NM				1	7	2			10	65.9
F_2 NM/IR 36	5	7	11	15	17	15	14	7	91	63.6
F_1 NM/IR 36			1	5	4				10	59.9
F_2 IR 36/KN			4	6	25	16	39	5	95	75.4
F_1 IR 36/KN							3	5	8	91.2
F_2 Calotoc/NM			1	3	3	6	25	49	87	87.6
				Tests at TARC, Okinawa, 1982						
KN					1	4	14	6	25	85.1
IR 36			1	1	3	5	7	3	20	78.0
Calotoc (CT)					2	10	3		15	76.8
F_2 IR 36/KN		2	10	14	26	25	22	5	105	68.9
F_2 IR 36/NM	3	5	8	12	13	11	10	2	64	51.9
F_2 CT/IR 36	21	5	12	12	19	15	13	6	103	55.0

progeny of fertile plants, and from the semi-sterile plants, many semi-sterile plants were reproduced along with nearly normal plants.

In the following generations, the tests were continued only with the cross of Nihonmasari/IR 36, and fertile as well as semi-sterile plants were chosen in each of the F_3 lines to test their progeny. The results are shown in Table 5-3. From the lines which were developed from fertile F_2 plants, only a few of the semi-sterile plants were found in F_4 except in one of the F_3 lines (H3) which might have been semi-sterile but phenotypically rated as fertile plants in the F_2. On the other hand, the progeny from semi-sterile F_2 plants segregated a large number of plants with normal fertility in the F_4 generation (Table 5-4). Many lines which were derived from semi-sterile plants with a spikelet fertility of 30–40 percent in F_2 and F_3 generations, segregated many plants with a nearly normal fertility. In the F_5 generation, those plants which showed a fertility of 30–40 percent from the F_2 to F_4 were chosen, and tested (Table 5-5). It was shown that the level of the fertility was enhanced in every line and many plants with normal fertility were recovered. Most of the plants with semi-sterility were genetically heterozygous, and recovered normal plants.

Table 5-2. Distribution of spikelet fertility in the F_3 lines from high or low fertility plants in F_2

F_3 lines	Fertility of parent %	No. of plants in each fertility class %								Total	Mean %
		-30	-40	-50	-60	-70	-80	-90	-100 %		
					IR 36/Nihonmasari						
H 1	92.6	1	1	1	1	8	7	2		21	65.3
H 2	91.5		1	1		1	12	7		22	74.8
H 3	90.0		1			3	5	9	2	20	77.3
H 4	90.0			1		2	2	3		8	73.5
H 5	89.2						2	4	1	7	82.3
L 1	32.5	1	1	5	1	5	5	1	1	20	60.6
L 2	32.3	9	2	6	1	1		1		20	35.0
L 3	25.3	1	2	5	7	3	3	1		22	55.9
L 4	22.3	2	1	5		4	4	1		17	57.0
L 5	30.1	3	4	4	3	2	5			21	50.5
					Nihonmasari/IR 36						
H 1	90.6				3	4	9	4	2	22	74.7
H 2	92.9					3	6	12	1	22	78.9
H 3	89.9		3	5	2	3	4			17	56.0
H 4	90.7				2	5	9	4		20	71.9
H 5	87.9			2	1	6	8	5		22	70.5
L 1	32.3	1	4	1	3	5	6	1		21	57.9
L 2	35.9	2	6	5	4	1	1	1		20	48.4
L 3	31.0	1		3	4	4	6	1		19	61.8
L 4	41.4		1	2	2	8	5	2		20	66.4
L 5	30.1		2	1	2	6	4			15	60.4

Sterility of progeny from Javanica/Indica or Javanica/Japonica crosses. Four Javanica varieties of the 'Banten' group, namely, Loktjan, Padi Segutuk, Para Doon Dawa and Cicih Balanak were chosen. All of them showed normal spikelet and pollen fertility with Japonica testers, and normal pollen fertility and semi-sterility of spikelet with Indica testers. For each of these Javanica varieties, F_2 populations of Japonica (Tohoku 127)/Javanica, and IR 36/Javanica were tested to evaluate the spikelet fertility. The results are shown in Table 5-6. The F_2 plants from Japonica/Javanica crosses showed a nearly normal fertility except a few plants with a lower fertility, while segregation into normal fertility and lower fertility was found in the F_2 of Indica/Javanica crosses. Based on the genetic analyses, the F_1 sterility of the Indica/Javanica is known to be caused by the loss of female gametes carrying a Javanica allele, but the Javanica allele can be conveyed through pollen. Therefore, in the F_2 generation, half of the individual plants are expected to be semi-sterile. Table 5-6 shows the expected results.

Table 5-3. Distribution of spikelet fertility in F_4 lines from high fertility plants in F_2 (Nihonmasari/IR 36)

F_4	Fertility %		No. of plants in each fertility class								Total	Mean
lines	F_2	F_3	-30	-40	-50	-60	-70	-80	-90	-100%		%
H1-16	90.6	92.6					3	8	8	2	21	79.4
-21		90.4					2	10	9	1	22	79.9
- 6		76.2				3	2	5	8	4	22	78.1
-10		75.7				1	2	13	6		22	75.1
-18		59.3			2	5	4	5	6		22	68.7
-19		58.5	1		2		5	7	7		22	71.2
H2- 1	92.9	91.1				1	5	4	9	3	22	79.0
-12		89.1					1	7	12	2	22	82.5
- 3		84.3						3	16	3	22	84.9
- 7		81.4				1	2	8	9	2	22	79.0
- 2		62.2					1	4	15	2	22	81.9
- 9		63.4					3	15	4		22	75.5
H3-14	89.9	77.0	1	2		6	2	3	1		15	58.6
-21		79.6	1	1	1	1	2	2	3	3	14	69.4
-10		57.7				2	2	6	7	1	18	77.6
-22		56.4			2	4	2	4	4	1	17	68.9
- 2		37.3		1	6	2	1			1	11	52.2
- 3		35.2	3	3	7						13	37.0
H4- 2	90.7	82.2			1		4	4	9	3	21	79.0
-17		86.0						5	9	7	21	85.1
- 1		75.6				2	4	5	7	5	23	78.7
- 3		72.8					4	9	6		19	75.7
- 6		5 .1				3	4	10	5		22	72.1
- 7		52.5			1	3	3	8	5	2	22	73.9
H5- 8	87.9	84.7					1	6	14	2	23	83.8
-11		87.4				1	5	9	8		23	75.4
- 2		73.6					5	7	8	2	22	78.5
- 3		74.4					6	14	2		22	73.8
- 5		48.2				7	8	5	2		22	66.8
-21		48.9	1	1	2		6	7	5		22	67.6

Table 5-4. Distribution of spikelet fertility in the F_4 lines from low fertility plants in F_2 (Nihonmasari/IR 36)

F_4	Fertility %		No. of plants in each fertility class								Total	Mean
lines	F_2	F_3	-30	-40	-50	-60	-70	80	-90	-100%		%
L1- 6	32.3	81.8					6	5	11	1	23	76.9
-16		74.5					5	11	4		20	74.5
- 4		61.9				6	6	10			22	67.1
- 8		62.3			4	6	8	3			21	60.2
-13		30.7				3	5	9	4		21	71.7
-18		25.5			1	1	3	6	8		19	74.3
L2- 7	35.9	82.4					1	9	11	1	22	81.2
- 9		75.4						3	8	11	22	88.5
-18		40.7		1	9	4		1	6	2	23	62.9
-22		40.2			4	2	2	4	6	3	21	72.4
-10		27.8	2	1	1	1	7	3	1		16	61.1
-11		27.4		5	3	5	4	2	2		21	56.0
L3- 9	31.0	75.7					3	11	9		23	77.1
-21		87.3				1	2	3	16	1	23	81.8
- 2		57.4	1		1	2	4	4	7	2	21	72.3
-18		58.0		1	1	2	6	6	2		18	66.1
- 6		42.1					4	1	11	6	22	85.0
-11		23.9		1	3	2	2	4	2		14	62.3
L4-10	41.4	85.7						4	7	11	22	87.3
-17		83.9					2	5	14		21	81.0
- 6		67.2		1			2	3	14	2	22	80.5
-14		66.7				1	2	7	10		20	78.0
- 5		39.9					4	5	10	4	23	81.2
-18		41.7		1	1	2	1	3	9	6	23	79.3
L5-10	30.1	76.7				1		1	10	11	23	87.9
-16		71.2			1	1	2	7	10	2	23	78.8
- 8		66.9					2	9	6	6	23	82.4
-18		67.1			1		4	4	10	2	21	78.1
-11		38.4			1	1	1	3	1		7	69.0
-14		-										

Table 5-5. **Distribution of spikelet fertility of F_5 lines from low fertility plants in F_4 (Nihonmasari/IR 36)**

F_5 lines	Fertility of parent %	No. of plants in each fertility class								Total	Mean %
		-30	-40	-50	-60	-70	-80	-90	-100 %		
L1-18-10	41.2			2	2	10	6	2		23	65.0
L2-10- 6	27.5	1	3	4	2	3	1	2		16	53.6
- 7	38.1	3	2	2	4	3	2	4	1	21	57.5
- 8	28.2		1	2	1	6	11	2		23	69.0
-14	47.8	2	2	7	5	3	4			23	50.7
L2-11- 2	35.3		1	6	8	7	1			23	55.3
- 4	37.2	1	1	5	8	7	1			23	54.6
- 9	33.7	1	2	8	1	5	3	3		23	56.6
-12	36.9			3	12	1	5	2		23	61.7
-14	31.8		1	8	6	2	3	3		23	58.1
L4-18-13	38.2			5	2	5	5	5		22	66.9
-15	43.1		1	7	1	3	3	7	1	23	66.0
L5-16- 8	50.0				4	8	9	2		23	69.7
L5-18- 4	49.4	4	3	5	4	3	3			22	47.5

Table 5-6. **Distribution of spikelet fertility in F_2 populations of Indica-Javanica and Japonica-Javanica crosses**

Crosses	No. of plants in each fertility class									Total	Mean %
	-20	-30	-40	-50	-60	-70	-80	-90	-100 %		
Tohoku 127/Loktjan	1		3	4	5	12	11	6	3	45	66.4
IR 36/Loktjan	6	5	1	3	5	5	5	1		31	46.4
Tohoku 127/Padi Segutuk				1	3	4	6	4	3	21	73.4
IR 36/Padi Segutuk	2	7	6	5	8	3	1	2	1	35	45.8
Tohoku 127/Para Doon Dawa			1	3		9	16	10	3	42	73.9
IR 36/Para Doon Dawa	4	3	9	3	8	7	2	1	1	38	47.4
Tohoku 127/Cicih Balanak				2	7	11	14	8	2	44	70.3
IR 36/Cicih Balanak	2	1	10	9	12	4	8			46	51.1

All the Javanica varieties belong to 'Banten' group. IR 36 and Tohoku 127 were used as an Indica and a Japonica tester, respectively.

Test of the progeny from the WCV/Indica and WCV/Japonica variety. Despite the normal fertility of the F_1 hybrids between Ketan Nangka and an Indica tester or a Japonica tester, a large number of semi-sterile plants were segregated in their F_2 populations, as shown in Table 5-1. The semi-sterile plants were segregated at a high frequency in the cross of WCV/IR 36, while a small number of the semi-sterile plants were produced in the F_2 of WCV/Japonica.

Out of the F_2 populations, five each of normal and semi-sterile plants were chosen from the F_2 of Nihonmasari/Ketan Nangka and IR 36/Ketan Nangka. Each of the F_3 lines was tested for their segregation of the sterility (Table 5-7). Based on the results, those semi-sterile plants in the F_2 of IR 36/Ketan Nangka were found to produce a large number of semi-sterile plants, while the ratio of semi-sterile plants was relatively small in Nihonmasari/Ketan Nangka. Some F_4 lines were further tested (Table 5-8).

Table 5-7. Distribution of spikelet fertility in F_3 from low and high fertility plants in F_2 of tester varieties/Ketan Nangka

F_3 lines	Fertility in F_2 %	No. of plants in each fertility class								Total	Mean %
		-30	-40	-50	-60	-70	-80	-90	-100 %		
					Nihonmasari/Ketan Nangka						
1-14	91.3		2	1			8	6	1	18	73.3
2-13	95.6					1	6	4	1	12	79.9
3- 6	91.5			1	2	4	8	4	2	21	73.7
5- 5	95.2			1	2	1	6	11	1	22	77.3
6- 5	96.4				1	5	2	4	10	22	82.2
3-12	73.6	1	1	3	8	7		1	1	22	56.9
4-14	71.1				2	4	12	3	1	22	74.1
5-21	78.8			1	1	4	5	4	2	17	74.2
9-14	75.9			3	5	3	4	1	1	17	63.9
10- 4	72.9			1	3	6	3	1		14	65.0
					IR36/Ketan Nangka						
1-18	88.1				4	4	7	6		21	72.5
4-19	68.4	1	1	2	2	5	4	1	1	17	62.4
6- 2	93.6				1	7	3	5	4	20	77.8
8-16	93.2						1	6	7	14	90.0
8-17	99.0				2	4	6	7	2	21	76.6
2-12	49.6	2	3	2	5	6	3	1		22	56.4
3- 6	46.2	7	2	3	3	5	2			22	44.5
5-17	40.8	6	3		4	6	1			20	45.4
7- 9	48.3	4	3	2	5	3	3	2		22	52.8
7- 8	52.6				5	4	7	3	1	20	71.1
					Control						
IR 36				1	1	3	5	7	3	20	78.0
Ketan Nangka						1	4	14	6	25	85.1
Calotoc						2	10	3		15	76.8
F_2 IR36/Ketan Nangka			2	10	14	26	25	22	5	104	68.9

50 was less than 10 percent, when the plants with less than 70 percent fertility are assumed to be semi-sterile, while, more than 80 percent of the plants in the F_2 of N8M/IR 36 were semi-sterile. Therefore, it is concluded that the majority of the semi-sterile plants in F_2 generation of Indica-Japonica crosses are produced by the allelic interaction at the locus *S-5,* and the sterility can be mitigated by the introduction of the $S\text{-}5^n$ gene.

Discussion

The fact that most of the semi-sterile plants in the F_2 population of the Indica-Japonica cross produced progeny lines which segregate semi-sterile as well as fertile plants can be attributed to the heterozygotes of $S\text{-}5^i/S\text{-}5^j$. The same genetic model predicts that if the $S\text{-}5^j$ is replaced by $S\text{-}5^n$, the level of the sterility in the F_2 would be reduced remarkably. This prediction was validated by the evidence from the cross of Shin-kei 8544/IR 50, in which the majority of the F_2 plants showed normal fertility.

Also the same model account for the difference in the level of spikelet fertility between the F_2 population of Javanica/Indica and that of Javanica/Japonica. In the latter crosses the level of fertility was much higher than that in the Javanica/Indica crosses which were derived from semi-sterile F_1 hybrids.

Among the factors which determine the level of the sterility in later generations, the imperfect elimination of the gametes carrying $S\text{-}5^j$ should be noted. In Indica-Japonica crosses, even if all the female gametes carrying the $S\text{-}5^j$ allele were to be eliminated in the F_1 plants, the genotype of $S\text{-}5^i/S\text{-}5^j$ would be reproduced at the ratio of 50 percent in the F_2 generation, because $S\text{-}5^j$ can be conveyed through pollen. The experimental results suggested that there are still many plants of the $S\text{-}5^i/S\text{-}5^j$ genotype in the F_2 population. It should be also noted that not all of the female gametes with $S\text{-}5^j$ seemed to be eliminated in the F_1 of $S\text{-}5^i/S\text{-}5^j$ due to some genetic mechanism which partially suppresses the elimination of $S\text{-}5^j$ gametes.

A mechanism to suppress the gamete elimination was also suggested in the test of F_2 populations of WCV/Indica crosses, where a large number of semi-sterile plants appeared, and proved to be heterozygous, despite the normal spikelet fertility of the F_1 hybrids. This fact suggests the role of some latent sterility-causing loci, which seem to be suppressed in the F_1, but revealed in the F_2 generation. A similar fact was also found in the cross of Taichung 65//Taichung 65/Panbira, in which a genic effect associated with the alk^+ locus of Panbira seemed to suppress the sterility-causing heterozygote linked closely with the *A* locus.

It is likely that there are many sterility suppressing alleles in rice varieties. Due to that effect, some F_1 may show a nearly normal fertility, although there would be segregation of semi-sterile plants through successive generations. Further tests are necessary to clarify the genetic nature and the extent of such sterility-suppressing genes. However, the fact that the single replacement of $S\text{-}5^j$ by $S\text{-}5^n$ greatly reduced the sterility in the F_2 generation suggests that the use of the $S\text{-}5^n$ gene can be an efficient means to obtain fertile 'Indica-Japonica crosses'.

Summary

The effect of allelic interaction on the sterility in early generations was tested. Firstly, normal plants and semi-sterile plants were chosen from the F_2 population of IR 36/Nihonmasari and Nihonmasari/IR 36. A few plants with a low fertility were

Table 5-8. Distribution of spikelet fertility in F_4 lines in the cross of Nihonmasari or IR 36/Ketan Nangka (1983, first season)

F_4 lines	Fertility of parent %	No. of plants in each fertility class -30	-40	-50	-60	-70	-80	-90	-100%	Total	Mean %
					Nihonmasari/Ketan Nangka						
3-12-16	80.9		1		1	5	13	3		23	70.7
3-12- 2	29.6	2	2	12	3		1			20	44.7
9-14- 1	78.5				2	6	5	1		14	68.6
5-21- 2	45.1	1	2	2	5	8	2			20	56.1
10- 4- 4	46.3	3	6	7		2	1	2		21	45.7
					IR 36/Ketan Nangka						
3- 6-12	74.6	3		3	3	3	3	4		19	59.3
3- 6- 7	23.4	4	1	6	3	1				15	43.3
5-17- 1	71.7	2	1	2	3	4	8	2		22	62.9
5-17-17	23.6	5	3	3	5	3	2			21	46.5
7- 9-16	85.7			1	2	5	11	3		22	71.0
7- 9-12	30.6	4	3	4	3	3		2		19	45.8

The results indicate that there is at least one more locus for the allelic interaction for semi-sterility, which was not revealed in the F_1 hybrid of IR36/Ketan Nangka, perhaps due to an unidentified suppressor gene. Such an effect of suppressor gene for the allelic interaction was also suggested in the cross of Taichung 65//Taichung 65/Panbira (Table 5-5).

Effect of S-5^n allele incorporated into Japonica background. Several experimental lines were developed to incorporate the Ketan Nangka's S-5^n gene. Of these, Shin-kei 8544 was derived from a cross of Akihikari/NK4, and morphologically not different from Japonica varieties. NK4 is a line selected from a F_6 bulk population of Nihonmasari/Ketan Nangka. F_1 hybrids between Shin-kei 8544 and some Indica varieties, such as IR 36, Nanjing 11, Suweon 258 and Milyang 23 showed normal fertility.

Spikelet fertility of the F_2 population of Shin-kei 8544/IR 50 was examined together with a F_2 population of N8M/IR36. N8M is a dwarf mutant of typical Japonica type from Norin 8 (Table 5-9). The ratio of semi-sterile plants in the F_2 of Shin-kei 8544/IR

Table 5-9. Level of spikelet sterility in F_2 hybrids between an Indica tester IR50 and a Japonica line with S-5^n gene from Ketan Nangka

Crosses	Total No. of plants	Ratio of plants in each fertility class (%) -30	-40	-50	-60	-70	-80	-90	-100%
Shin-kei 8544/IR 50	143	1.4	1.4	1.4	2.1	0.7	9.1	33.6	50.3
N8M/IR 36	152	53.3	5.3	10.5	9.2	4.6	7.2	5.3	4.6

Shin-kei 8544, a line from Akihikari/NK4 hybrids S-5^n gene instead of S-5^j.
NK4 is a line selected from F_6 population of Nihonmasari/Ketan Nangka.
N8M is a dwarf mutant from Norin 8, a typical Japoncia rice.

found in the progeny of fertile F_2 plants, and from the semi-strile F_2 plants, many semi-sterile plants were reproduced along with nearly normal plants. Furthermore, fertile as well as semi-sterile plants in each of the F_3 lines were chosen and tested. Many lines which were derived from semi-sterile plants with a spikelet fertility of 30–40 percent in the F_2 and F_3 generations segregated many normal plants in the F_4 generation. In the F_5 generation, those plants which showed a fertility of 30–40 percent from F_2 to F_4 produced many normal plants. Therefore, it was concluded that most of the plants with semi-sterility are genetically heterozygous, and recover many normal plants.

Secondly, some of the F_2 populations of hybrids between Javanica (Banten group) and Indica, and between Javanica (Banten group)/Japonica were compared to study the relationship between the level of F_1 sterility and that in the F_2 generation. The F_2 plants from Japonica/Javanica crosses showed a nearly normal fertility except a few plants with a low-fertility, while segregation into normal fertility and lower fertility was found in the F_2 of Indica/Javanica crosses, as expected by the alleles at the *S-5* locus.

Despite the normal fertility of the F_1 hybrids, semi-sterile plants were segregated at a high frequency in the F_2 population of WCV/IR 36. Also, a small number of the semi-sterile plants were produced in the F_2 of WCV/Japonica. Those semi-sterile plants in the F_2 of IR36/Ketan Nangka were found to produce a large number of semi-sterile F_3 plants, while the ratio of the semi-sterile F_3 plants was relatively small in Nihonmasari/Ketan Nangka. Some F_4 lines were found to produce semi-sterile plants. The results suggested that there is at least one more locus for the allelic interaction for semi-sterility, which was not revealed in the F_1 hybrid of IR36/Ketan Nangka due to an unidentified suppressor gene in the F_1 hybrids.

Lastly, the effect of the *S-5ⁿ* allele incorporated into a Japonica background was examined as a part of the breeding program to utilize the *S-5ⁿ* gene. With the use of apiculus color as a marker gene, it was easy to select some lines which carry the *S-5ⁿ* gene. Several experimental lines were developed to incorporate the Ketan Nangka's *S-5ⁿ* gene. Of these, Shin-kei 8544 which was derived from a cross of Akihikari/NK4 was morphologically not different from Japonica varieties. NK4 is a line selected from a F_6 bulk population of Nihonmasari/Ketan Nangka. F_1 hybrids between Shin-kei 8544 and some Indica varieties, such as IR36, Nanjing 11, Suweon 258 and Milyang 23 showed normal fertility. Further, the ratio of semi-sterile plants in the F_2 of Shin-kei 8544/IR50 was extremely low, indicating that *S-5ⁿ* can be effective for reducing sterility in wide crosses.

General Discussion

Varietal classification. After the description by Kato (1930) of *indica* and *japonica* subspecies in *Oryza sativa,* on the basis of the fertility of F_1 hybrids, Terao and Mizushima (1939) classified six Japanese, three American and two Javanese varieties into Group I (Japonica), five Indian native varieties into Group II, and four varieties including Tetep and Dahanala into Group III. They found a clear F_1 sterility in the hybrids betwen the Group I and III. But, the sterility of the hybrids between the Groups II and III was not clearly low, and similar to that between the Groups I and II. Therefore, Group II was considered to be an intermediate type.

Later, Matsuo (1958) proposed three varietal groups, A, B and C, the center of which was assumed to be Japan, Java and India, respectively. He concluded that A and B belong to the Group I classified by Terao and Mizushima, and C to Groups II and III, as it was difficult to separate Group II from Group III by morphological criteria.

Morinaga and Kuriyama (1958) tested five 'ecological groups' of cultivated rice, i.e. Japanese rice, Aus, Aman, Bulu and Tjereh. Based on the fertility of the F_1 hybrids between these groups, they concluded that the Bulu and Aus varieties are intermediate between Indica and Japonica varieties. But they did not test the F_1s between Bulu and Aman or Tjereh, and there was a methodological problem. They simply averaged the data of individual crosses to get the mean F_1 fertility between two groups. Accordingly, after averaging the data over the Aus group as a whole an intermediate value of F_1 fertility was obtained despite the intra-group diversity.

Javanica varieties. The designation 'Javanica' was redefined and given by Morinaga (1954) to the Indonesian native varieties, 'Bulu' (awned) and 'Gundil' (awnless). The comparative characteristics of the Bulu and Gundil, and Tjereh (Indicas) varieties were described earlier by Van der Meulen (1941). Matsuo (1952)'s description of the B group was in good agreement with Van der Meulen's. Although Morinaga (1958, 1968) used later the name Bulu instead of Javanica, it seems better to call the whole group Javanica, since no comprehensive local term is known for both Bulu and Gundil.

The three wide-compatibility varieties (WCVs) found in the present tests, i.e. Calotoc, Ketan Nangka and CPSLO 17 were included into Javanica rice. Five other compatibility types were found in the Javanica group. The majority of the varieties belong to the 'Banten' group, which showed fertility with the Japonica tester and spikelet semi-sterility with the Indica tester. Moreover, Hawara-Geporeck in the preliminary test and two photoperiod-nonsensitive varieties in the test of stress-tolerant varieties showed the compatibility of the Japonica type.

In the stress-tolerant varieties, the majority of the varieties from the Philippines or Indonesia belonged to the typical Indica type, and were strongly photoperiod-sensitive. Photoperiod-sensitivity is an essential trait for lowland rice cultivation, and may characterize the compatibility of Indica type, whereas, the characteristics of Javanica varieties can be related to the adaptability to upland cultivation.

Based on the fertility of F_1 hybrids between two Javanica varieties, reproductive barriers did not seem to have developed within the group despite their differential compatibility with Indica and Japonica testers. It is interesting to note that all of these compatibility types including the Indica and Japonica testers show normal fertility with the WCVs. In this context, they all can be a group of varieties with a link to the WCVs.

Aus varieties and ambiguity of so-called Indica group. The Aus varieties were recognized as an intermediate group between the Indica and Japonica varieties (Terao and Mizushima, 1939; Morinaga and Kuriyama, 1958). The diversity of compatibility types within this group was revealed in their cross to Indica and Japonica testers. Varietal diversity was also indicated in other traits, such as alkali-digestion, phenol reaction, heariness of glumes, cold tolerance and so on. However, the F_1 hybrids between different compatibility types of the Aus varieties generally showed a good level of fertility. Further, the Aus varieties showed sterility in their crosses to Ketan Nangka and other WCVs. In the analyses of isozymes by Nakagahra (1978), varieties from Bengal to the Indian Subcontinent were clearly different from the rest.

From these evidences, the Aus varieties as a whole seem to be different from other varietal groups. Some native or improved varieties from the South Indian region showed a similarity to Aus varieties, suggesting that the compatibility of the Aus type can be widely found among the varieties in the Indian Subcontinent.

Therefore, under the name of Indica, there are two groups of cultivated rice, although most of the varieties tested in Japan as Indica are Aus varieties because of their short growth duration. If the group represented by Aus is called Indica type, then the rest of the so-called Indica varieties including the strongly photoperiod-sensitive varieties with the compatibility of Indicas in the Philippines and Indonesia and Hsien of China should be called by another name. Nakagahra (1978) re-classified a part of this group as *sinica* (Hsien).

Perhaps most important is the understanding that there are an Indian Subcontinent group represented by Aus, and another group including the rest of so-called Indica varieties. Japonica and Javanica groups may not be far from this, if their compatibility to WCVs is considered as a criterion.

Genetic analyses of F_1 sterility. For a long time hybrid sterility in rice was attributed to some structural differences of chromosomes between Indica and Japonica types (Chandraratna, 1964). However, a genic explanation has been widely accepted for the past three decades. There are two contrasting genetic explanations: Oka (1953, 1964, 1974) proposed a model of duplicate recessive gametophytic lethals; Kitamura (1962, 1963) assumed that Indica and Japonica varieties posses Fs^i/Fs^i and Fs^j/Fs^j alleles (*Female semi-sterility*), respectively at a locus, and the gametes carrying Fs^j are to be aborted in the maternal genotype of Fs^i/Fs^j. In this system, the genotype for WCVs can be given as Fs^n/Fs^n, assuming that Fs^n/Fs^i and Fs^n/Fs^j are fertile. A similar case is described in tomato by Rick (1966). Sano *et al.* (1979) reported a case of gamete abortion by allelic interaction in the crosses between isogenic lines from a variety of *Oryza sativa* and a strain derived from *Oryza glaberrima.*

Based on the experimental results, the one-locus model as proposed by Kitamura was proved to be valid. At a locus $S\text{-}5$ the allelic interaction of $S\text{-}5^i/S\text{-}5^j$ was shown to cause partial abortion of female gametes carrying $S\text{-}5^j$.

Oka (1954, 1958) assumed that the wide-compatibility varieties have more dominant alleles than those with a narrow compatibility, and that each of reproductive barriers were caused by two independent mutations. In reality, however, mutations at the $S\text{-}5$ locus seem to be able to produce new alleles antagonistic to each other, and to develop reproductive barriers. Of them, the role of $S\text{-}5^i$ is of interest, because it eliminates the opposite allele together with adjacent genes, and forms an exclusive set of traits. Once the $S\text{-}5^i$ allele had been spontaneously produced in a primitive, undifferentiated varietal grop including Javanica and Japonica types, then that genotype carrying the $S\text{-}5^i$ would have proliferated with adjacent genes *Lm* for photoperiod-sensitivity (Yokoo and Kikuchi, 1980), alk^+, Wx^a for high amylose (Sano, 1984) and others. This process can be called as 'genic introgression' of Indica type.

In practice, the exclusion of the *alk* — *wx* segment of Japonica or Javanica varieties from the hybrids with Indicas should be taken into account, as these genes determine the cocking quality of rice.

Citing the parentage of American WCVs such as Century Patna 231 and CPSLO 17, Jennings (1966) argued that the progeny from Indica-Japonica crosses would result in wide compatibility. Theoretically, the two-locus model predicts such outcome, however, the genetic model confirmed in the present study ruled out such a possibility. The donor of $S\text{-}5^n$ to CPSLO 17 must be some Javanica WCVs in the Philippines. Some previous experiments on the progeny genotypes from distant crosses (Nagamatsu and Omura, 1960; Oka, 1957) should be reexamined in the light of the valid genetic model.

According to the two-locus model for F_1 sterility by Oka (1974), it is expected that the majority of the progenies of Indica/Japonica crosses should be of wide-compatibility type due to the survival of the gametes which possess two of dominant alleles in the putative gamete lethal system. But such type is not easily found in actual experiments. Accordingly, Oka (1974) assumed a system of competitive fertilization among gamete genotypes, and ascribed the scarcity of wide compatibility type to a low competitive ability of the gametes of the dominant alleles. With regard to Oka's assumption, it is of interest that anther culture lines derived from an Indica/Japonica cross produced only the compatibility types of Indica or Japonica parent (Fujimaki *et al.* 1986). This result clearly indicates that there is no gamete for the wide-compatibility in the Indica/Japonica cross.

On the basis of the one locus theory for F_1 sterility, an important rule can be deduced that a cross between two different types each with a narrow compatibility cannot synthesize a wide-compatibility type. Another rule can also be deduced that a cross between two different types each with a narrow compatibility hardly allow simultaneous establishment of the two types in its progeny because of gamete abortion, as it is in Indica/Japonica crosses. Therefore, a new compatibility type can be fixed only in the background of wide-compatibility, as it is in the genotype of S^n/S^i or S^n/S^j. Actually, there are a series of different compatibility types in the Aus group. These types did not reveal clear sterility or gamete abortion in the crosses within the group. More or less similar cases are found in the Javanica group. In these group, differentiation of the compatibility types is detected by inter-group crosses. Differentiation of 'gametophyte genes' in Japonicas, which are reported by Maekawa *et al.* (1981) and Maekawa and Kita (1985), suggests that some new mutants of compatibility type are latently conserved in the Japonica group.

Pollen sterility. Mori *et al.* (1973) reported that the segregation of some markers, *wx, C* and *alk* was significantly biased from the normal ratio when F_1 hybrids between distantly related varieties were crossed as pollinators. The bias was observed even when the F_1 hybrids with morphologically normal pollen were chosen as pollinators. Recently, Maekawa (1981, 1985) reported another series of gametophyte genes. In his experiment, F_1 hybrids between Japonica varieties were tested and their level of fertility was normal. In the above cited papers, the distorted segregation was attributed to competitive fertilization among functionally normal pollen. And, the presence of gametophyte genes which control the selective fertilization of gametes was assumed. Nakagahra *et al.* (1972) and Nakagahra (1972) reported the presence of two gametophyte genes near the loci of marker genes, *bc* and *dl.* Nakagahra *et al.* (1974) also reported the presence of a gametophyte gene at a locus near *wx, C* and *alk.* Nakagahra (1981) reported the presence of another gametophyte gene in the third linkage group. In these cases, the relation between the distoted segregation and the level of pollen fertility was not examined.

In our experiments, the marker genes, *bc* and *dl* which were reported as the markers of gametophyte genes were found to be related in some way to pollen fertility, although they were not directly indicative of the pollen sterility gene, *Sc* which was reported by Kitamura (1962, 1963). Likewise, the marker gene, *Ph* was related to the level of pollen fertility.

Through several steps of repeated hybridization, a genic effect similar to that of the $S\text{-}5^n$ gene for spikelet fertility was assumed for the pollen fertility in the F_1 hybrids between Calotoc and Indica or Japonica testers. In these crosses, the ratio of pollen-fertile *versus* pollen-semi-sterile plants was biased significantly. The distorted segregation can be better understood as the expression of an allelic interaction, as it was seen for female gametes.

Iwata *et al.* (1964) reported the presence of a gametophyte gene which was considered to control selective fertilization of gametes in the cross between an atomic-bomb-irradiated mutant and a normal variety. In that case, the pollen sterility may be affected by more than one locus, as it was shown in some crosses in our studies.

F_1 sterility between Aus and other varieties. The compatibility type of Aus varieties seemed to be different from that of Indica, Javanica, and Japonica types. Therefore, the question of whether the Aus varieties have different alleles at the *S-5* locus or not was the next target of our analyses. Due to some methodological difficulties, only a few cases of clear indication of allelic interaction were found despite the many crosses tested.

A clear case of pollen sterility was related to the genotype of A/A^+ in the linkage group III, and a sterility-suppressing genic effect was related to the genotype of *alk/+* in the cross of Taichung 65//Taichung 65/Panbira. Thus, the locus for the semi-sterility-causing allelic interaction is tentatively designated as *S-6*, which is located close to the *A* locus.

Another important fact found in the cross of Ingra/Ketan Nangka//CPSLO 17 is that the hybrid sterility between WCV and Aus varieties is caused by an allelic interaction at a locus, *S-7* near the *Rc* (Red pericap) locus in the IV linkage group. A set of multiple alleles may be found at this locus. By the differentiation of the alleles at the locus, the compatibility between the Aus group and the rest of the varietal groups may be explained.

Three semi-sterility-causing loci were found in the present studies. Of these, *S-6* near *A* locus is tentative, because the function can be interpreted by the system of *a* and *I* (Kitamura, 1962, 1963). Perhaps, at these loci many varieties may possess neutral or identical alleles, the pairing of which does not cause gamete abortion.

Sterility in early generations. In Indica-Japonica crosses, most of the semi-sterile plants in the F_2 population and in successive generations produced progeny lines which segregate semi-sterile as well as fertile plants. These results confirmed the genetic model according to which a majority of the female gametes carrying $S\text{-}5^j$ is eliminated from the semi-sterile genotype of $S\text{-}5^i/S\text{-}5^j$ but the $S\text{-}5^j$ allele can be conveyed through pollen. Therefore, in the progeny of semi-sterile plants, $S\text{-}5^i/S\text{-}5^j$ and $S\text{-}5^i/S\text{-}5^i$ can be reproduced at the rate of 1:1. It should be also noted that not all of the female gametes with $S\text{-}5^j$ are eliminated in the genotype of $S\text{-}5^i/S\text{-}5^j$.

The genetic model validated by our work predicts that if the $S\text{-}5^j$ allele of a Japonica variety is replaced by $S\text{-}5^n$, the level of sterility in the F_2 would be reduced remarkably in Japonica-Indica crosses. This prediction was confirmed by the experiments on Shin-kei 8544 (a Japonica line with $S\text{-}5^n$)/IR 50, in which the majority of the F_2 plants showed normal fertility. Therefore, the sterility problem in wide crosses can be solved by the use of the $S\text{-}5^n$ allele. The allele can also be used for hybrid seed production with distantly related varieties.

One of the facts that cannot be explained by the allelic interaction is the sterility fixed in homogeneous status in the later generations. Perhaps, there are other types of sterility (Kitamura, 1962, 1963; Oka and Doida, 1962; Yokoo, 1984).

Summary and Conclusion

A total of 80 varieties including Aus and Bulu varieties was crossed to an Indica and a Japonica tester variety, and the fertility of the F_1 hybrids with Indica or Japonica testers was examined to determine the compatibility types of each variety.

In the initial test, Calotoc, CPSLO 17 and Ketan Nangka were confirmed to be 'compatible' both to Indica as well as to Japonica varieties. These varieties were designated as wide-compatibility varieties (WCVs).

Out of 24 Indonesian varieties, a majority of 15 varieties was classified into one group by their high pollen fertility both with the Indica and Japonica testers, the normal spikelet fertility with the Japonica tester, and the clear semi-sterility with the Indica tester. Six varieties showed sterility with both of the testers. Only one variety, Padi Bujang Pendek exhibited normal fertility in its hybrids with Indica and Japonica testers. One variety, Hawara-geporeck in the preliminary test seemed to belong to Japonica type based on its compatibility.

The F_1 hybrids between different compatibility types in the Javanica group showed generally normal fertility with a few exceptions like Saba Enim.

Out of 14 varieties tolerant of environmental stress, two varieties insensitive to photoperiod showed the compatibility of Japonicas. The majority of ten varieties with strong photoperiod-sensitivity was found to be of the Indica type.

In the test of Aus varieties, two varieties, Aus 373 and Dular seemed to be widely compatible. Five varieties showed relatively good fertility with the Indica and Japonica testers. Seven varieties showed the compatibility of the Indica type. Nine varieties showed the compatibility type of the Japonica tester. The rest of the 18 varieties were not classified into any definite category.

Generally, the fertility of the hybrids between two Aus varieties was found to be normal regardless of the compatibility types of the parent variety.

In the hybrids between some Aus varieties and WCVs, the fertility of the F_1 hybrids was very low with a few exceptions, such as Dular and other two varieties. In the additional tests, some varieties from South India were not definitely classified into Indicas nor into Japonicas. The F_1 hybrids between them and Ketan Nangka showed lower fertility, suggesting their similarity to Aus varieties. Two Bhutan varieties seemed to be WCV.

The varietal group of Aus was found to include various compatibility types in terms of F_1 sterility, and the types of compatibility are likely to be different from those of Indica, Javanica, and Japonica types. Other evidences also suggest that the varieties in the Indian Subcontinent are different from the rest of varietal groups.

The F_1 semi-sterility in wide crosses of cultivated rices has been explained by two contrasting genetic models: a model of duplicate recessive gametophytic lethals (two-locus model) and another model of one-locus heterozygosity.

To test the validity of the proposed models, three-variety crosses were designed to differentiate the hypothetical roles of two independent loci for F_1 sterility. In the paired crosses of Akihikari/Ketan Nangka//IR 36, and IR 36/Ketan Nangka//Akihikari, the genotype, wx/wx^+ and C/C^+ clearly showed a significantly higher fertility than the reverse genotype, wx^+/wx^+ and C^+/C^+. The two marker genes *wx* and *C* are known to be closely linked, and possessed by Ketan Nangka. Therefore, the fertility was assumed to be controlled by the $S\text{-}5^n$ gene from Ketan Nangka. The experimental results were explained assuming that the Indica and Japonica testers have a $S\text{-}5^{i}$ and $S\text{-}5^{j}$ allele, respectively, and that the genotype of $S\text{-}5^{i}/S\text{-}5^{j}$ is semi-sterile while $S\text{-}5^{n}/S\text{-}5^{i}$ and $S\text{-}5^{n}/S\text{-}5^{j}$ are fertile. All the three WCVs were found to possess a common $S\text{-}5^{n}$ gene at the same locus near *C*, which was named *S-5* following *S-4* which had been reported for interspecific hybrids.

The experimental results indicated that the majority of gametes carrying the allele from the Japonica parent, $S\text{-}5^{j}$ was aborted in the F_1 genotype of $S\text{-}5^{i}/S\text{-}5^{j}$.

With Ketan Nangka's $S\text{-}5^{n}$ allele, it was also found that the spikelet sterility in the F_1 between Indica testers and Javanica varieties was due to the heterozygosity at the same locus. And, in the F_1 between the Indica tester and Javanica testers, the majority of the gametes with *C* of Javanica varieties was shown to be eliminated. As a whole, the compatibility relation among Indica, Javanica and Japonica varieties was ascribed to the allelic interaction of the multiple alleles at the *S-5* locus. The origin of reproductive barriers should be based on the differentiation of alleles at the locus. The genotype of $S\text{-}5^{i}$ may result in genic introgression forming a set of genes adjacent to this locus.

The effect of the WCV's wide compatibility in terms of pollen fertility was traced through three-variety crosses and several steps of repeated hybridization.

In the Ketan Nangka crosses, the ratio of pollen-fertile plants was not different between the two crosses, i.e. IR 36/Ketan Nangka//Japonica variety and Japonica variety//IR 36/Ketan Nangka.

In the Calotoc crosses, reciprocal differences were observed: the cross of IR 36/Calotoc//Japonica variety segregated a larger number of fertile plants than its reciprocal, Japonica variety//IR 36/Calotoc. Further, the pollen-fertile plants from the cross of IR 36//Japonica/Calotoc were again crossed to the Japonica tester as pollinator. Out of the progeny of these crosses, the pollen-fertile plants were further crossed to the Indica tester as pollinator.

The segregation of a certain number of pollen-fertile plants after each of the successive crosses indicated that the WCVs have a Sc^{n} genotype. And, Indica and Japonica testers may possess Sc^{i} and Sc^{j}, respectively, as has been reported by Kitamura (1962, 1963). When the cross was in the format of $Sc^{i}//Sc^{n}/Sc^{j}$, the majority of the progenies was fertile, whereas, when the cross was in the format of $Sc^{j}//Sc^{n}/Sc^{i}$, the majority of the progeny was sterile. Therefore, a portion of Sc^{n}-pollen is likely to be aborted in the genotype of Sc^{i}/Sc^{n}, and a portion of Sc^{j}-pollen in the genotype of Sc^{j}/Sc^{n}.

In further experiments, Japonica testers with additional marker genes, i.e. *lg* (liguleless in the second linkage group), and *bc* (brittle culm) and *lop-2* (dl-lopped leaf -2) of the XI linkage group were tested in addition to *alk*, C^{+}, Ph^{+}, and so on. Some experimental Japonica lines with these markers were crossed to Indica testers in backcrossing experiments, and the relation between these markers and pollen or spikelet fertility was examined.

The fact that the Ph/Ph^{+} genotype was related to a higher fertility than the Ph^{+}/Ph^{+} genotype suggested that a gene near this marker has a mitigating effect on the sterility.

In other crosses, the decrease of the dosage of *bc* was related to higher fertility. The concurrent effect of the dosage of *Ph* and bc^{+} is related to the higher level of the spikelet fertility. Significant decrease of male gametes carrying *bc* was confirmed when the F_1 hybrids were used as pollinators. There seems to be a pollen-sterility-mitigating gene near the *bc*$^+$ locus.

Based on these results, the distorted segregation of marker genes which has been attributed to selective fertilization due to gametophyte genes seemed to be better understood by the presence of an allelic interaction similar to that in $S\text{-}5^i/S\text{-}5^j$ and some genes which suppress the interaction.

In the genetic analyses of the compatibility of Aus varieties, backcrosses of Japonica/Aus varieties//Japonica were made, and in other cases, Aus varieties or WCV were backcrossed. In the B_1F_1, the relation between the level of the fertility and the marker gene was analyzed.

In the cross of Taichung 65 (Japonica)//Taichung 65/Panbira, the pollen sterility seemed to be related to the genotype of A^+/A, but suppressed by a genic effect related to *alk*$^+$ from Panbira. Similarly, a slightly less significant relationship was found between these genotypes and the level of spikelet sterility. The locus, *S-6* near *A* seemes to be responsible for the F_1 sterility between Aus and Japonica varieties. Likewise, the frequency of *Ps*$^+$ and *dl* was extremely reduced in the cross of Tareba (Japonica)/Acharbhog. The frequency of gametes jointly carrying these markers was reduced remarkably.

An Aus variety, Aus 373 initially seemed to be one of the WCVs. The spikelet fertility in the cross of Aus 373/IR50//Akihikari was related to the genotype of C/C^+, suggesting the allelic interaction of $S\text{-}5^i/S\text{-}5^j$ and the linkage of $S\text{-}5^n$ and *C* in Aus 373.

A clear case of allelic interaction was found, when an Aus variety with red pericarp, Ingra was used in the cross of Ingra/Ketan Nangka//CPSLO 17, in which the cross between Ketan Nangka and CPSLO 17 did not show hybrid sterility, and the sterility could only be traced to the combination of Ingra and the two WCVs. In this cross, the level of spikelet fertility was clearly related to the *Rc* locus in the Linkage Group VI. Therefore, one of the bases for the pronounced hybrid sterility between Javanica and Aus varieties can be attributed to an allelic interaction at this locus, which is designated as *S-7*.

The effect of the allelic interaction on the sterility in early generations was also tested. It was found that most of the semi-sterile plants in early generations of Indica-Japonica hybrids are genetically heterozygous, and recover many plants with normal fertility. These results confirmed the genetic model as follows: from the semi-sterile genotype of $S\text{-}5^i/S\text{-}5^j$, a majority of gametes carrying $S\text{-}5^j$ are eliminated, but the $S\text{-}5^j$ allele can be conveyed through pollen. Therefore, in the progeny of semi-sterile plants, $S\text{-}5^i/S\text{-}5^j$ and $S\text{-}5^i/S\text{-}5^i$ can be reproduced at the rate of 1:1.

The F_2 plants from Japonic/Javanica crosses showed nearly normal fertility except for a few plants with a low-fertility, while the segregation into normal fertility and lower fertility was found in the F_2 of Indica/Javanica crosses.

Despite the normal fertility of the F_1 hybrids, semi-sterile plants were segregated at a high frequency in the F_2 population of WCV/IR 36. Also, a small number of semi-sterile plants was produced in the F_2 of WCV/Japonica. Additional tests were continued until F_4. The results suggested that there is at least one more locus for the allelic interaction for sem-sterility, which was not revealed in the F_1 hybrid of IR36/Ketan Nangka due to an unidentified suppressor in the F_1 hybrids.

Lastly, the effect of the $S\text{-}5^n$ allele incorporatd into a Japonica background was examined as a part of the breeding program to develop widely compatible lines. It was easy to find lines which possess the $S\text{-}5^n$ gene by the use of the marker gene, *C* (apiculus color). Of these, Shin-kei 8544 was derived from a cross of Akihikari/NK4 (a line selected from a F_6 bulk population of Nihonmasari/Ketan Nangka). F_1 hybrids between Shin-kei 8544 and some Indica, such as IR 36, Nanjing 11, Suweon 258 and Milyang 23 showed normal fertility. Furthermore, the ratio of semi-sterile plants in F_2 of Shin-kei 8544/IR 50 was extremely low, indicating that $S\text{-}5^n$ can be effective for reducing sterility in Indica-Japonica crosses. Further studies on hybrid sterility would be facilitated by the use of such lines as Shin-kei 8544.

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Appendix I. Characteristics of Aus varieties tested

Varieties	F_1 fertility %				Grain length /width	Alkali-diges-tion	Phenol reac-tion	Cold toler-ance	Seed source
	With Japonica		With Indica						
	Poll.	Spik.	Poll.	Spik.					
Aus 373	94.3	88.0	89.6	91.3	2.52	1	-	2	Acc. 29158
Dular	97.1	83.7	89.6	86.7	3.10	1-2	-	5	200041
Akula	80.0	85.6	93.1	90.7	2.93	1	+	5	VT 75
As 35	70.0	94.4	89.6	91.3	2.76	2-3	+	3	200028
DV 149	49.8	85.1	94.2	86.1	2.31	2	-	5	Acc.8538
Panbira	66.7	84.8	90.9	92.1	2.11	2	-	4	VT 64
Bhutmari 36	95.8	53.5	87.6	93.2	2.68	1	+	4	210014
Aus 402	55.6	59.8	98.8	85.1	2.89	1	-	2	Acc.29186
CH 972	58.2	30.5	94.7	84.8	2.48	2	-	4	200011
CH 1039	58.4	13.2	98.2	96.3	2.50	2-3	+	2	200033
Chakila	53.2	77.5	92.9	89.8	2.61	1	+	3	Acc.27540
Jhanji	85.4	60.8	96.2	93.7	2.58	1	+	3	200061
Kele	54.2	69.4	92.2	88.2	2.62	1	+	4	210013
Kumari	59.6	69.8	92.3	93.4	3.39	1	-	4	210004
DJ 123	93.0	87.2	69.4	70.9	2.33	2	+	5	Acc.8455
H 2871	95.8	93.1	44.5	35.8	3.17	2	+	4	200001
Kaladumai	94.0	94.7	58.4	81.1	2.72	1	+	3	200040
M 142	99.6	94.3	44.8	70.3	2.73	1	+	3	200014
Marichibati	98.2	90.8	86.4	48.1	2.37	7-8	-	1	CAES
Parambu Vattan	98.6	89.1	28.7	34.0	1.97	7-8	-	1	200049
R 11	97.9	88.5	85.8	62.3	2.49	8	-	1	200035
RDR 7	91.3	92.1	40.7	26.5	3.32	1-2	+	4	200027
Satika	96.1	81.8	83.3	54.4	2.63	1	+	5	210003
As 20-1	84.5	89.1	90.8	77.2	2.76	2	+	3	200022
Aus 371	97.9	64.2	93.2	38.1	2.76	1	-	4	Acc.29175
N 136	92.9	36.8	87.4	70.8	4.13	1	-	5	200052
Charnack	48.6	32.1	92.5	39.5	3.56	1	-	3	200060
DV 16	85.5	19.1	90.4	70.2	2.21	1	-	1	Acc.8812
Ingra	48.2	61.4	97.4	68.3	2.72	1	+	5	Acc.27552
DV 32	83.8	93.7	48.1	35.4	2.43	1-2	+	2	Acc.8818
DV 52	81.1	91.8	68.4	83.7	2.60	2	+	3	Acc.8828
Lepudumai	71.0	93.3	49.9	80.0	3.64	1	-	5	200044
DV 34	69.9	84.0	67.5	54.8	2.35	1-2	+	2	Acc.8820
Kataktara	66.4	86.9	57.6	43.1	2.18	6-7	-	1	200048
Bolun	49.5	64.9	82.7	88.4	2.45	1	+	5	Acc.27534
Porang	96.7	52.3	45.4	67.3	2.55	1-2	+	4	Acc.27577
Achar Bhog	78.0	71.1	75.1	62.0	2.59	2	-	2	Acc.25826
Aus 430	53.2	41.5	69.9	46.0	3.00	1	-	2	Acc.29212
Dharial	75.7	32.8	76.8	22.4	2.05	2	+	1	210006
DZ 151	72.2	22.2	59.0	70.2	2.62	2	-	4	Acc.8541
Marichi Buti	81.5	61.5	74.2	50.0	2.14	1-2	+	2	200059

Note : Alkali-digestion ; 1 (hard) — 8 (soft).
Cold-tolerance ; 1 (tolerant) — 5 (susceptible).