Multiple Alleles Controlling F₁ Sterility in Remote Crosses of Rice (*Oryza sativa*)

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We reported previously that Indonesian rice varieties belonging to the so-called Javanica varieties could be classified into some different types in respect to F₁-sterility relationships with a set of Indica and Japonica testers. Firstly, in this study, we observed that the F₁ plants between these different types were fertile with a few exceptions. Secondly, to look into the genetic basis of the sterility of the F₁ hybrids between a variety, Penuh Baru II and Indica or Japonica testers, we made three-varietal crosses involving Penuh Baru II, a "wide-compatibility" variety Ketan Nangka, and IR 36 or IR 50 (Indica tester). The progeny of the three-varietal crosses showed an association of spikelet fertility with certain gene markers. The segregation pattern for the spikelet fertility was explained by a model of one-locus allelic interaction. It was postulated that the Japonica tester as well as Penuh Baru II have the same allele *S-5^j* while the Indica tester has *S-5ⁱ* at the *S-5* locus belonging to linkage group I, and that female gametes with *S-5^j* are aborted in plants with the genotype of *S-5ⁱ/S-5^j*. Ketan Nangka was found to have a wide-compatibility allele *S-5ⁿ* which does not confer sterility in combination with other alleles. The F₁ sterility of Penuh Baru II with Japonica tester appeared to be controlled by sterility genes other than those at *S-5* locus. The wide-compatibility gene *S-5ⁿ* can be useful in the breeding of Indica-Japonica crosses and also in developing Indica-Japonica F₁ varieties.

KEY WORDS : *Oryza sativa*, sterility, gamete abortion, "wide compatibility", remote cross, wide cross.

Introduction

The sterility in remote crosses of rice is unique in comparison with that in other crops. In most cases, F₁ seeds can be easily obtained, but the F₁ plants of remote crosses show semisterility. The semisterility in early generations can be attributed to heterozygosity of genes. Another type of semisterility is also found frequently in homozygous lines (KITAMURA, 1961, 1962 ; OKA and DODA, 1962 ; YOKOO, 1984).

Previous workers showed that some varieties gave high F₁ fertilities in their crosses to Indica as well as to Japonica varieties (TERAO and MIZUSHIMA, 1939 ; MORINAGA and KURIYAMA, 1958 ; HEU, 1967). Reviewing these papers, IKEHASHI (1982) emphasized the need for systematic screening and utilization of wide-compatibility varieties (WCVs) to overcome the sterility barrier in remote crosses. If the genic control of the wide compatibility is simple, the wide-compatibility gene can be utilized for the breeding of Indica-Japonica crosses and for developing Indica-Japonica F₁ varieties (ARAKI *et al.* 1986).

In our previous study (IKEHASHI and ARAKI, 1984), we have screened 80 varieties with Indica and Japonica tester varieties to identify widely compatible types. Calotoc, Ketan Nangka and CPSLO 17 were found to be widely compatible, producing fertile F₁ plants with both Indica and Japonica tester varieties. We also found that Penuh Baru II and

a few other varieties produced semisterile F_1 plants with both of Indica and Japonica testers. In order to learn about the genetic control of the particular F_1 -sterility relationship of Penuh Baru II, we made three-varietal crosses involving this variety, Ketan Nangka, and IR 36 or IR 50 (Indica tester), following the design as used by IKEHASHI and ARAKI (1986). The pattern of variations in spikelet fertility observed in the progeny was compared with two different models of sterility genes, one being the duplicate gametic lethal model (OKA, 1953, 1974), and the other, the one-locus allelic interaction model (KITAMURA, 1961, 1962). The result showed that the behavior of spikelet sterility in these varietal hybrids fitted the second model, as is reported in this paper. The term "compatibility" in this paper implies a measure of relationship as shown by the spikelet fertility of F_1 hybrids between two varieties, and the gene symbols are used after the proposal for rules of gene symbolization by Rice Genetics Cooperative (KINOSHITA, 1984).

Materials and Methods

For testing the wide compatibility of a variety, IR 36 and IR 50 were used as Indica testers, and Akihikari and Tohoku 127 were used as Japonica testers. The F_1 hybrids between Indica and Japonica testers showed F_1 semisterility. Ketan Nangka was used as a WCV which produced fertile F_1 hybrids with both Indica and Japonica testers (IKEHASHI and ARAKI, 1984).

To analyze the genetic basis of F_1 sterility in remote crosses of rice, three-varietal crosses were made following our previous scheme (IKEHASHI and ARAKI, 1986) as follows: Ketan Nangka/Penuh Baru II//IR 50, Ketan Nangka/IR 36//Penuh Baru II, and Ketan Nangka/Akihikari//Penuh Baru II. A backcross of Kamairazu/Penuh Baru II//Kamairazu was used to test the gamete elimination in F_1 hybrids. Ketan Nangka is a WCV and has marker genes *C* (apiculus color, chromogen for anthothyanin) and *wx* (glutinous endosperm). Penuh Baru II showing F_1 sterility with both Indica and Japonica testers has colorless apiculus (C^+ , formerly *c*) and non-glutinous endosperm (wx^+). IR 36 and IR 50, both being colorless in apiculus and having non-glutinous endosperm, were used as Indica testers assuming that they have the same F_1 sterility genes. Akihikari and Tohoku 127 were used as Japonica tester, and Kamairazu is a Japonica variety having marker genes, *bc* (brittle culm) in the XI linkage group and *alk* (alkali digestion) near the *C* locus. Spikelet and pollen fertility of all the hybrid plants were measured at the Okinawa Branch of Tropical Agriculture Research Center (TARC) at Ishigaki island.

Results

Fertility of F_1 hybrids between two different types of Javanica varieties The so-called Javanica varieties can be classified into some groups; Penuh Baru group, Banten group, Ketan Nangka group and so on, in respect to their F_1 -sterility relationship with the Indica and Japonica testers (IKEHASHI and ARAKI, 1984). It was found that the Banten group (Banten and Gamah) showed F_1 spikelet sterility with the Indica tester and F_1 spikelet fertility with the Japonica tester, and that the third group including Ketan Nangka and others showed F_1 fertility with both Indica and Japonica testers. Accordingly, the varieties of the third group were referred to as WCVs (IKEHASHI and ARAKI, 1984).

Table 1. Pollen and spikelet fertility of F₁ plants from crosses between varieties of "Penuh Baru II" group and testers

	Fertility %				Seed Source (NIAR)
	1981		1983		
	Pollen	Spikelet	Pollen	Spikelet	
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	
Tohoku 127/Penuh Baru II	75.4	44.0			
Akihikari/Penuh Baru II			75.6	30.9	
K. 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	
Tohoku 127/Page Leoh	83.6	65.3			
Akihikari/Page Leoh			70.9	77.6	
K. 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	
Tohoku 127/Sigabe Taon	67.5	63.7			
Akihikari/Sigabe Taon			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	
Tohoku 127/Simanuk	83.0	57.2			
Akihikari/Simanuk			70.8	84.6	
K. Nangka/Simanuk			97.6	79.0	

Note : Ketan Nangka is abbreviated as K. Nangka.

Firstly, in the present experiment, the Penuh Baru group including Penuh Baru II, Page Leoh, Sigabe Taon and Simanuk were confirmed to show F₁ spikelet sterility with both Indica and the Japonica testers, although the sterility of F₁ hybrids between the latter three varieties and Japonica tester was of low degree (Table 1). Secondly, all the crosses between the two varieties of these different groups were found to produce fertile F₁ plants (Table 2).

Three-varietal crosses including Penuh Baru II The progeny plants of three-varietal crosses, Ketan Nangka/Penuh Baru II//IR 50 and Ketan Nangka/IR 36//Penuh Baru II, were distinguishable into fertile and semisterile classes bordering on about 75% spikelet fertility. In both of the crosses, most of the plants with the gene *C* or *wx* belonged to the fertile class and those with *C*⁺ or *wx*⁺ by and large belonged to the semisterile class (Table 3). This suggests that *C* and *wx* were linked with the wide-compatibility gene derived from Ketan Nangka, in the same manner as was found in our previous experiment (IKEHASHI and ARAKI, 1986). The same wide-compatibility gene, which was symbolized *S*-5ⁿ, was found to control the fertility in the present crosses. Accordingly, the F₁ sterility between Penuh Baru II and the Indica tester can be attributed to the allelic interaction at the *S*-5 locus.

On the other hand, the F₁ sterility between Penuh Baru II and Japonica varieties did not seem to be controlled by the alleles at the *S*-5 locus, as it showed no relation

Table 2. F_1 fertility of crosses between Javanica varieties

Crosses	Fertility %	
	Pollen	Spikelet
With Banten Group (1984, second season)		
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
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
Within Penuh Baru Group (1984, first season)		
Sigabe Taon/Simanuk	97.7	95.6
Sigabe Taon/Penuh Baru II	98.1	94.5
Simanuk/Penuh Baru II	96.4	93.4

Table 3. Distribution of spikelet fertility in three-variatal crosses with Ketan Nangka and Penuh Baru II

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

Note : Numbers underlined show assumed recombinants.

* After IKEHASHI and ARAKI (1986)

with the marker genes C and wx in the cross of Ketan Nangka/Akihikari//Penuh Baru II (Table 3).

These results indicate that the F_1 -sterility relationships among the Indica, Japonica and Javanica varieties are largely controlled by an allelic interaction of multiple alleles

Table 4. Distributions of spikelet fertility in the progeny of Kamairazu/Penuh Baru II//Kamairazu

Genotype	No. of plants in each fertility class								Total	Mean %
	-30	-40	-50	-60	-70	-80	-90	-100%		
<i>bc/bc</i>	1	4	2	5	2	4	7	8	33	70.3
<i>bc/+</i>	1		3	3	6	9	6	8	36	73.9
<i>alk/alk</i>	2	3	4	4	2	7	6	10	38	70.5
<i>alk/+</i>		1	1	4	6	6	7	6	31	74.3

at the *S-5* locus. However, the F₁ sterility between Penuh Baru II and Akihikari seems to be caused by other gene(s) at another locus.

Gamete elimination test in F₁ hybrid between a Japonica variety and Penuh Baru II
The authors (IKEHASHI and ARAKI, 1986) reported that most of female gametes with *S-5^j* were eliminated in the genotype of *S-5ⁱ/S-5^j* due to an allelic interaction at the *S-5* locus. Therefore, it is expected that the progeny of the semisterile plants heterozygous for a marker genes linked with the *S-5* locus show a distorted segregation for the marker gene. To identify the genotype of gametes which could be eliminated in the semisterile hybrid between a Japanese variety and Penuh Baru II, the backcrossed progeny of Kamairazu/Penuh Baru II//Kamairazu was tested (Table 4). In the backcrossed progeny, the plants homozygous and heterozygous for the two marker genes, *alk* and *bc* were found in an approximately 1:1 ratio, and there was no significant difference in fertility between the homo- and hetero-zygotes (Table 4).

This suggested that the F₁ sterility between Kamairazu and Penuh Baru II was not due to the allelic interaction at the *S-5* locus, which was near the *alk* locus, but was controlled by other gene(s). This is in accord with the fertility distribution observed in Ketan Nangka/Akihikari//Penuh Baru II, in which the fertility was not related to the markers *C* and *wx*.

Therefore, it is likely that Akihikari and Penuh Baru II possess the same allele, *S-5^j*. This assumption may be verified, because many of the Javanica varieties showed the same type of F₁ sterility relationship as of Japanese varieties, and the *S-5* allele of Banten and Gamah behaved like the *S-5^j* in the gamete elimination test (IKEHASHI and ARAKI, 1986).

In all these experiments, pollen fertility was recorded for individual plants, but its variation showed no relationship with the marker genotypes. Therefore, the data for the pollen sterility are not presented in this paper.

Mapping of the S locus Since the distribution of spikelet fertility was continuous and subject to environmental fluctuation, the recombinants between the *S-5* gene and the markers were not always determinable. In Ketan Nangka/Penuh Baru//IR 50 and Ketan Nangka/IR 50//Penuh Baru, the range of spikelet sterility was separated clearly into low and high classes (Table 3). In these crosses recombination values between *S-5* and the two markers were estimated. The maximum likelihood estimates of the recombination values were 3.8~4.3 percent between *S-5* and *C* and 23.1~26.1 percent between *S-5* and *wx*.

Discussion

The sterility of hybrids in rice was once attributed to structural differences of chromosomes between the Indica and Japonica types (CHANDRARATNA, 1964, Chap. 5). Later, it was attributed to genic differences. There are two different models of sterility genes, one being the duplicate gametic lethals proposed by OKA (1953, 1964, 1974), and the other one-locus allelic interaction proposed by KITAMURA (1961, 1962).

KITAMURA concluded that Indica and Japonica varieties possessed genes for female semisterility, F_s^i and F_s^j (female sterility gene) at a locus, and male semisterility gene, S_c^i and S_c^j (scanty pollen) at another locus, and male and female gametes carrying F_s^j and S_c^j , respectively, are aborted when the genotype of maternal plants is heterozygous for the respective gene. A similar case has been found in tomato by RICK (1966). SANO *et al.* (1979) and SANO (1983) reported gamete abortion due to allelic interaction in crosses between isogenic lines of a variety of *Oryza sativa* and of *O. glaberrima*.

The previous authors, however, have not reported an allele which does not confer sterility. A neutral allele $S-5^n$ is a new finding by the present authors (IKEHASHI and ARAKI, 1986). According to our previous studies, the $S-5$ locus has at least three alleles, $S-5^n$, $S-5^j$ and $S-5^i$. In the heterozygotes $S-5^i/S-5^j$, gametes with $S-5^j$ are aborted due to an allelic interaction, but gametes with $S-5^i$ are not aborted in the heterozygote. If the penetrance of genic effect is perfect, the heterozygotes $S-5^i/S-5^j$ will show 50 percent sterility and the genes linked with $S-5^j$ will be significantly eliminated from the progeny. When $S-5^n$ is present in the maternal plant, however, no gamete is aborted. Therefore, the varieties possessing $S-5^n$ are identified as the WCVs. The gametes aborted by such an allelic interaction may be female or male, or both. In the present case, only the female gametes were affected by the $S-5$ locus. The phenomenon of the wide compatibility was also found in an Asian wild rice (*O. rufipogon*) strain (HINATA and OKA, 1962).

According to the duplicate lethal gene hypothesis, the WCVs are expected to have plus alleles at two independent loci, $s-a^+ \cdot s-b^+$; and Penuh Baru II and IR variety may be assumed to have $s-a^+ \cdot s-b$ and $s-a \cdot s-b^+$, respectively. And, gametes with $s-a \cdot s-b$ produced in the F_1 hybrid between Penuh Baru II and IR variety would be aborted.

Then, in the pair of three-varietal crosses, namely, WCV/Penuh Baru II//IR variety and WCV/IR variety//Penuh Baru II (assuming IR 50 and IR 36 to have the same sterility genes), when the marker gene C is linked with one of the two loci, it can be associated with the sterility only in one of the paired crosses. For instance, $(s-a^+ - C/s-a^+ - C^+ \cdot s-b^+/s-b) \times s-a - C^+ \cdot s-b^+$ may be the genotype of the first three-varietal cross, and $(s-a^+ - C/s-a - C^+ \cdot s-b^+/s-b^+) \times s-a^+ - C^+ \cdot s-b$ that of the second cross. In this case, sterility should be associated with apiculus colorless only in the second cross. Therefore, the association of sterility with the markers in both of the paired crosses as observed in the present experiment cannot be explained by the duplicate gametic lethal hypothesis. This is plausible evidence for rejecting the duplicate gametic lethal hypothesis in explaining the results of the present experiment. On the basis of the linkage relations with the markers C and wx , the locus of wide-compatibility gene found here must

be *S*-5, which was reported previously by the authors (IKEHASHI and ARAKI, 1986).

The multiple alleles at the *S*-5 locus seems to play a significant role in varietal differentiation of rice. If the *S*-5ⁱ allele is produced spontaneously in a varietal population containing diverse genotypes, it will increase autonomously together with the genes linked with it. Such genes would be *alk*⁺ for alkali digestion, *Se*-1 for photoperiod-sensitivity (*Lm* by YOKOO et al. 1980), *Est*-2^s for esterase-2 S (NAKAGAHARA, 1984), *Wx*^a for high amylose content (SANO, 1984).

It was reported that experimental lines derived from anther culture of an Indica-Japonica cross showed F₁ fertility with either Indica or Japonica parent (FUJIMAKI *et al.* 1986). This suggests that there was no gamete of *s*-a⁺·*s*-b⁺ genotype among those lines from the Indica-Japonica cross. According to the one locus theory for F₁ sterility, it can be deduced that a cross between two different types each with a "narrow compatibility" cannot synthesize a wide-compatibility type. Therefore, the allele like *S*-5ⁿ will be useful for mitigating sterility in hybridization breeding involving remote crosses like breeding by Indica-Japonica crosses and for developing Indica-Japonica F₁ varieties.

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イネの遠縁交配における F_1 不稔性を支配する複対立遺伝子

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先に著者ら (1984) は, Aus および Bulu 群を含む栽培稻 80 品種を, インド型 (IR 36 もしくは IR 50) と日本型 (ニホンマサリ もしくは アキヒカリ) の検定品種にそれぞれ交配して F_1 不稔性を検討し, Ketan Nangka, Calotoc, CPSLO 17 などが両種の検定親と正常稔性を示す「広親和性」品種 (WCV) であることを報告した. この実験に供試したインドネシアの Javanica 品種 24 のうち, 15 品種は, インド型検定品種と F_1 不稔性を示し, 日本型とは稔性を示す群 (Banten 群) であり, 6 品種は, 両者と F_1 不稔を示す群 (Penuh Baru 群) であった.

しかし, これらのインドネシア品種群相互間の F_1 不稔性はよく分かっていなかったのでもうこれを調査した. Penuh Baru 群とした 4 品種は, いずれも Ketan Nangka と稔性を示した. Banten 群の代表とした Banten と Gamah は, Penuh Baru 群の品種と正常稔性を示した. また, Penuh Baru 群相互間でも正常稔性がみられた. この結果からこれらインドネシア品種相互間の F_1 は不稔性を示さないと結論された.

次に, Penuh Baru 群としたものはインド型と日本型の双方と F_1 不稔性を示すので, これに関与する遺伝子座が既報 (IKEHASHI and ARAKI, 1986) の第 1 連鎖群に属する S-5 座にあるかどうかを検討した. この群から稈先色のない Penuh Baru II を選び, その品種の F_1 不稔性を, IKEHASHI and ARAKI (1986) の方法で分析した. すなわち, インド型の検定品種として IR 36 と IR 50 を, 広親和性品種 (WCV) として Ketan Nangka を用いて, WCV/Penuh Baru II//IR 品種と WCV/IR 品種//Penuh Baru II という一対の「三品種交配」を行った. ここで, はじめの F_1 は正常稔性を示す組合せである. これらの三品種交配の後代の種子稔性を個体別に調査したところ, 稔性群と半稔群は大体区別され, 稔性群では Ketan Nangka に由来する C (稈尖着色) および *wx* (糯性) の遺伝子を持つ個体が大部分を占め, これらの遺伝子と稔性遺伝子との連鎖を示した (Table 3).

もし Ketan Nangka の Penuh Baru II および IR 品種との F_1 稔性が, それぞれ独立の遺伝子により支配されるのであれば, その 2 遺伝子の効果は, 三品種交配において最後に, Penuh Baru II を交配するか, IR 品種を交配するかによって, 別の座の遺伝子の効果として識別されるはずである. 実際には双方の三品種交配を通じて同一の稔性遺伝子が C と密接に連鎖していることが認められた. したがって, これらの交配で稔性を支配する遺伝子は, 既報 (IKEHASHI and ARAKI, 1986) の Ketan Nangka の S-5ⁿ によるものと推定された.

Penuh Baru II と日本品種の間の F_1 は不稔性を示したが, その不稔性は C および *wx* の分離とは無関係であり, またその近傍の *alk* 遺伝子の分離も正常であった (Table 4). さらに, Penuh Baru II と稔性を示す Banten 群の品種が F_1 不稔遺伝子の行動について, 日本品種同様の行動を示すこと (IKEHASHI and ARAKI, 1986) を考慮すると, Penuh Baru II も S-5 座では S-5^j を持と推定され, その日本品種との不稔性は別の遺伝子によるものと考えられる. したがって, IR 品種の S-5 座の遺伝子を既報のように S-5ⁱ とすると, 今回の結果は, S-5ⁿ/S-5^j は稔性となり, S-5ⁱ/S-5^j は不稔となることを明瞭に示したものと考えられる.

以上の結果から, S-5 座においては, 少なくとも三種の複対立遺伝子があり, S-5ⁱ/S-5^j では対立遺伝子間の相互作用により, S-5^j を持つ雌性配偶子が排除されるため半不稔性を示すが, S-5ⁿ はこれら 2 つの複対立遺伝子に中立であると考えられる. 今後ハイブリッド品種の育成, 遠縁交配育種などにおいて, この不稔緩和遺伝子 S-5ⁿ の応用が期待される.