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STUDIES ON SCREENING AND GENETICS OF WIDE COMPATIBILITY IN RICE (*ORYZA SATIVA* L.)

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ABSTRACT

The hybrids of intersubspecific crosses involving indica (I) and japonica (J) rices show semisterility, while those with wide compatible varieties (WCVs) show normal fertility. A set of 42 varieties representing four varietal groups were evaluated in two diverse environments in testcrosses with three indica and japonica testers each for wide compatibility trait and its inheritance and relationship with the marker gene in four newly identified varieties were studied. Twelve varieties were identified as compatible, two intermediate and 28 narrow compatible varieties. Inheritance of WC in RP 1579-1704-1318, UPR 1279-1-4-1, Pusa 560-2-203-338 and UPRI-95-170 was controlled by single gene with dominance of wide compatibility over narrow compatibility. Wide compatibility gene (S_5^n) showed loose linkage with chromogen (C^+) gene on chromosome 6 with a recombination value of 34.2%.

Key Words : Rice, hybrid sterility, inheritance, wide compatibility genes, wide cross

The magnitude of heterosis depends on the degree of genetic distinctiveness and the combining ability of the parental lines used. Naturally, the indica/japonica hybrids would be expected to be the ideal cross combinations from the view points of adaptation and heterosis. Intersubspecific hybrids showed increased hybrid vigour in total dry matter and spikelet number. However, heterosis for grain yield is difficult to realise because of high degree of spikelet sterility [1-3].

Studies indicated certain rice varieties to produce fertile F_1 hybrids when crossed with both indica and japonicas [3-6]. Significance of this phenomenon was recognised by [7] who proposed a search for such varieties for use in overcoming the sterility barrier in indica/japonica crosses. Six rice varieties Aus 373, Dular, Colotoc, CP-SLO,

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Ketan Nangka and Padi Bujang Pendek showed normal spikelet fertility in F_1 crosses with indica-japonica varieties in Japan and were designated as wide compatible varieties (WCVs) [8]. Subsequently, they proposed the genetic basis for F_1 sterility and wide compatibility in 1986 [9].

Most of the WCVs used to overcome sterility of indica-japonica hybrids have been reported from Japan and IRRI and recently in the China mostly in aus and japonica varieties and their wide compatibility reaction in the indian environment was unknown. Also there is total lack of information on wide compatibility gene present in the improved indica genetic background. Since the spikelet fertility in some intervarietal hybrids is known to be influenced by environment (1-2, 10), it would be most desirable to test compatibility reaction of known WCVs in indian conditions prior to their utilization. Therefore, the present study reports on identification of elite rice varieties possessing the wide compatibility trait and the mode of inheritance and linkage relationships of wide compatibility gene(s) in the newly identified varieties with some markers to explore the prospects of its potential use in rice breeding.

MATERIALS AND METHODS

Screening for wide compatible varieties

Plant material : Forty two rice varieties of diverse origin belonging to four varietal groups [11], viz., Group I (indica), II (aus), VI (japonica) and V (*basmati*) were selected from the irrigated breeding programme of G.B. Pant University of Agriculture and Technology, Pantnagar, Four of these varieties viz., Dular, N22, Moroberekan and Palawan were known for their wide compatibility behaviour in the Philippines [12].

All crosses among 42 varieties and three testers each of indica (I) (IR 36, IR 50, IR 64) and japonica (J) (Akihikari, Taichung 65, Toyonishiki) were made in the glasshouse during 1994 ws. All possible control crosses between indica and japonica testers (I × J) and among indica (I × I) and japonica (J × J) testers were also made. A total of 252 crosses were completed.

All hybrids along with controls were transplanted for evaluation in the field at Hyderabad and in the glasshouse at Pantnagar during 1995 DS. For the field study, 21 day old seedlings of all the testcrosses alongwith the controls and parents were transplanted into a well puddled soil. Each test entry had 2.5 m long rows with an inter and intra row spacings of 20 cm each. In the glasshouse study, five day old seedlings germinated in seed germinator were transferred into pots. Three seedlings in each pot were maintained.

Recording data : Data on spikelet fertility was recorded visually from two good panicles from each of the five central plants in each test entry sampled at 25-30 d after flowering and hand threshed separately. The number of the total and fertile spikelets were counted with an Electronic Grain Counter. Spikelet fertility was computed and expressed in percentage for each test entry.

Statistical analysis : A t-test of unequal variances [13] was used to compare the significance of differences in the mean spikelet fertilities of six testcross hybrids for each test variety and the control crosses and parents.

Classification of varieties into compatibility groups : Classification of varieties into compatibility groups was done [12]. In the intervarietal group crosses, the test variety exhibiting mean hybrid spikelet fertility significantly higher than those of the indica/japonica F_1's but similar to indica and japonica tester parents or the intervarietal hybrid F_1 (I/I) were designated as WCVs. A test variety showing spikelet fertility of F_1 hybrids higher than the mean I/J F_1's but lower than the tester parents was designated as intermediate compatible (ICV). A test variety in crosses showing similar or lower spikelet fertilities than the I/J F_1's or showing larger differences in spikelet fertilities from the indica and japonica testers were grouped as narrow compatible varieties (NCVs).

Inheritance of wide compatibility

Parents used for the genetic analysis of wide compatibility trait were four out of the eight WCVs identified from the field and glasshouse screenings in the present study viz., RP 1579-1701-1318, UPR 1279-1-4-1, Pusa 560-2-203-338 and UPRI 95-170. A set of nine three variety test cross progenies and tester parents were evaluated for the inheritance of wide compatibility trait and its linkage with chromogen (C^+) for anthocyanin pigmentation in the apiculus.

Spikelet fertilities of test cross F_1 single plants were compared with I/J F_1s and control crosses. For calculating chi-square, the testcross F_1 single plants exhibiting spikelet fertility upto 40 per cent were taken as semisterile and those above 65 per cent fertile. The number of plants falling in the intermediate fertility range of 40-65% were equally divided between fertile and semi-sterile classes to minimize the bias in classification caused by environmental [2, 6, 14, 16] and other genetic sterility system (s) (10).

Linkage of the wide compatibility gene and the marker gene from three paired testcross progenies was computed as the proportion of observed frequencies of phenotypic recombinants to the parental types. In addition, % spikelet fertility of the marker genotypes were also compared to the contrasting genotypes by using t test.

RESULTS AND DISCUSSION

Screening for the wide compatibility genes

Mean % spikelet fertility of the crosses between the test varieties and the testers and their allocation into compatibility groups based on data from Hyderabad (field, dry season) and Pantnagar (glasshouse) are given in Table 1 for the indica (Group I) and Table 2 for the aus (Group II), basmati (Group V) and japonica (Group VI) varietal groups.

Based on isozyme polymorphism classification (11), we selected 42 elite rice varieties representing four varietal groups to screen for wide compatibility gene(s). Adequate genetic variation for WC trait in the collection was observed and the varieties were grouped into three compatibility groups of narrow, intermediate and wide compatibility based on % spikelet fertility in the inter-varietal group crosses (Tables 1 and 2). Similar groupings were also reported in Japan (4) and at the IRRI (12) working with diverse but different collection mostly involving traditional varieties.

Distribution of varieties into different compatibility groups indicated the narrow compatibility (NC) group to possess largest number of varieties (28) which included 24 indicas and two each of the basmati and japonica varieties. The intermediate compatibility (IC) group included only indica varieties RDR 536 and UPRI 95-172 in the field at Hyderabad and RDR 536 in the glasshouse screening at Pantnagar. Similar observations were previously made for other varieties of indica, japonica and basmati groups (2, 5, 8, 12, 15). The third group of wide compatible varieties (WCVs) had 12 varieties, eight of which belonged to indica viz., RP 1579-1701-1318, RP1967-20503-1241. UPR 1279-1-4-1, Pusa 560-2-203-338, Narendra 118, UPRI 95-169, UPRI 95-170 and UPRI 95-174 and two each to aus (N 22 and Dular) and japonica groups (Moroberekan and Palawan). Highly fertile F_1's in the intervarietal group crosses involving aus varietities, N 22 and Dular (Acc. 45616) and japonicas, Moroberekan and Palawan were also observed at IRRI (12), further confirming the wide compatible nature of these varieties. Rice variety Dular was also reported to be wide compatible by several workers in Japan and India [5, 8].

Effect of location on expression of wide compatibility trait : In the present study, an indica variety UPRI 95-172 was grouped as intermediate compatible variety evaluated at Hyderabad in South India under field condition, but narrow compatible at Pantnagar in the Northern part of the country in glasshouse conditions (Table 1). As the seed source of this variety studied in the two environments were same, its possibility to cause variation in the intervarietal group compatibilities is ruled out. Therefore, this differential expression of wide compatibility trait could be caused by genotype-environment interaction. Similar differences in performance was also

Table 1. Percent spikelet fertility of F_1 hybrids involving rice varieties of *indica* group with *indica* (I) and *japonica* (J) testers in field (light) and glasshouse (bold) environments at Hyderabad and Pantnagar, India, respectively

Varietal group/Variety	Mean spikelet fertility (%)								Compatibility group
	F_1 hybrid			Array mean	I × J F_1 mean	Tester parent mean	Difference from the array mean		
	I tester	J tester	Differences				I × J F_1 mean	Tester parent	
1	2	3	4	5	6	7	8	9	10
***Indica* (Group I)**									
BG 1321	85.8	56.2	29.6*	71.0	29.4	77.1	41.6*	-06.0^{ns}	NC
	76.1	43.3	32.8**	59.7	16.7	**73.1**	43.0*	**-13.4^{ns}**	**NC**
CU 8068	69.9	11.8	58.0**	40.8	30.7	77.3	10.1^{ns}	-36.4*	NC
	75.2	**26.1**	**49.1**	**45.7**	**17.1**	**72.7**	**28.6***	**-26.9^{ns}**	**NC**
GZ 1368-5-4	86.9	41.2	45.7**	68.7	33.8	77.6	34.8*	-08.9^{ns}	NC
	76.6	**25.5**	**51.0****	**51.0**	**18.5**	**72.2**	**32.5****	**-21.1^{ns}**	**NC**
IR 53915-137-3-2-3	78.9	33.6	45.2**	56.3	30.7	77.3	25.6*	-21.0^{ns}	NC
	73.6	**30.3**	43.2**	52.0	18.5	72.2	33.4**	-20.1^{ns}	NC
IR 53915-61-3-3-3	65.1	19.0	46.0**	42.0	30.7	77.3	11.3^{ns}	-35.2*	NC
	62.6	16.9	45.7**	39.7	18.5	72.2	21.2**	-32.4^{ns}	NC
RP 2217-4766-67-1	77.3	42.1	35.2*	63.2	33.8	77.6	29.4**	-14.4^{ns}	NC
	66.3	20.5	45.7**	43.4	22.4	70.5	20.9^{ns}	-27.1^{ns}	NC
RP 2327-318-869	81.4	53.0	28.4*	67.2	30.7	77.3	36.5**	-10.1^{ns}	NC
	68.6	26.6	42.0**	51.8	16.9	72.4	34.8*	-20.6^{ns}	NC
IR 1967-250-250	83.7	43.4	40.3*	67.6	28.3	77.2	39.2**	-09.6^{ns}	NC
	71.0	21.5	49.4**	46.3	17.4	71.8	28.8^{ns}	-25.5^{ns}	NC
RLR 33636	82.6	32.6	50.0*	57.6	32.4	78.3	25.1^{ns}	-20.7^{ns}	NC
	68.0	29.8	38.1*	48.9	16.2	73.3	32.6^{ns}	-24.4^{ns}	NC

1	2	3	4	5	6	7	8	9	10
RP 1579-1701-1318	83.5	85.7	–03.2^{ns}	84.	38.9	77.4	45.1**	06.6^{ns}	WC
	79.7	82.1	02.4^{ns}	80.9	17.4	71.8	63.9**	09.0^{ns}	WC
RP 1967-20503-1241	87.7	79.9	07.7^{ns}	83.5	24.5	76.6	59.0**	06.8^{ns}	WC
	70.4	67.8	02.6^{ns}	69.1	12.8	72.7	56.3**	–03.5^{ns}	WC
RDR 536	70.3	59.0	11.2^{ns}	63.5	35.5	77.0	28.0**	–13.4**	IC
	54.5	45.5	08.9^{ns}	50.0	22.4	70.5	27.5**	–20.5**	IC
Rasi	70.0	35.1	34.8*	52.5	30.2	77.9	22.3^{ns}	–25.3^{ns}	NC
	61.9	31.5	30.4*	46.7	20.0	72.9	26.6^{ns}	26.1^{ns}	NC
UPR 1279-1-4-1	77.7	84.4	–06.6^{ns}	80.4	28.3	77.2	51.1*	03.1^{ns}	WC
	65.8	64.4	01.3^{ns}	65.2	20.7	71.5	44.5**	–06.2^{ns}	WC
Pusa 560-2-203-338	74.1	70.7	03.3^{ns}	72.7	30.7	77.3	41.7**	–04.8^{ns}	WC
	76.0	66.3	09.7^{ns}	70.2	19.1	72.4	51.1**	–02.2^{ns}	WC
Ralghar	93.5	48.3	45.2**	75.4	28.2	76.7	47.2**	–01.2^{ns}	NC
	75.7	32.3	43.4**	54.0	16.7	73.	37.3^{ns}	–19.1^{ns}	NC
IR 1976-18-6-4-2	79.5	34.8	44.6*	57.2	29.4	77.1	27.8^{ns}	–19.9^{ns}	NC
	64.4	28.8	35.5*	46.6	16.7	73.1	29.8^{ns}	–26.5^{ns}	NC
UPRI 86-14	83.6	58.5	25.1*	73.6	29.9	76.7	43.6**	–03.1^{ns}	NC
	76.3	37.4	38.8*	56.8	12.8	72.7	44.0*	–15.8^{ns}	NC
Govind	81.1	51.0	30.1**	66.1	24.5	76.6	41.5*	–10.5^{ns}	NC
	64.8	39.4	25.4*	52.1	12.8	72.7	39.3*	–20.5^{ns}	NC
Manhar	72.7	40.2	32.5*	59.7	28.3	77.2	31.4**	–17.5^{ns}	NC
	81.3	22.8	58.5**	52.1	21.2	71.5	30.8^{ns}	–19.4^{ns}	NC
Jaya	78.8	42.7	36.0*	60.8	35.6	76.2	25.1^{ns}	–15.4^{ns}	NC
	60.8	30.4	30.3**	45.6	18.2	71.6	27.4^{ns}	–26.0^{ns}	NC
Narendra 1	74.8	41.8	33.0*	61.6	29.9	76.7	31.7*	–15.0^{ns}	NC
	65.1	29.0	36.0**	47.0	12.8	72.7	34.2^{ns}	–25.6^{ns}	NC
Narendra 80	73.3	51.0	22.3*	64.4	33.8	77.7	30.5**	–13.3^{ns}	NC
	70.2	28.7	41.5*	49.5	20.0	72.9	29.4^{ns}	–23.4^{ns}	NC

1	2	3	4	5	6	7	8	9	10
Narendra 118	79.4	79.8	–00.3^{ns}	79.6	29.9	76.7	49.6**	02.9^{ns}	WC
	67.6	66.0	01.6^{ns}	66.8	18.2	71.6	48.6**	–04.8^{ns}	WC
UPRI 95-168	72.7	43.9	28.7*	61.2	33.8	77.7	27.3**	–16.5^{ns}	NC
	68.7	34.7	34.0**	55.1	17.9	72.6	37.2**	–17.4^{ns}	NC
UPRI 95-169	87.0	82.5	–05.5^{ns}	85.2	33.8	77.7	51.4**	07.5^{ns}	WC
	70.8	66.7	04.0^{ns}	69.2	17.9	72.6	51.3**	–03.3^{ns}	WC
UPRI 95-170	85.2	82.4	02.8^{ns}	83.8	24.5	76.6	59.2**	07.1^{ns}	WC
	70.2	68.5	01.6^{ns}	69.3	12.8	72.7	56.5**	–03.3^{ns}	WC
UPRI 95-171	80.0	26.4	53.6**	58.6	29.9	76.7	28.6^{ns}	–18.1^{ns}	NC
	71.3	21.7	49.5**	51.4	16.9	72.4	34.4*	–20.9^{ns}	NC
UPRI 95-172	64.8	49.7	15.1^{ns}	57.3	30.2	77.9	27.1*	–20.6*	IC
	62.5	29.2	33.2*	45.9	12.8	72.7	33.1^{ns}	–26.8^{ns}	NC
UPRI 95-173	85.8	28.4	57.4**	62.8	28.2	76.7	34.5*	–13.8^{ns}	NC
	70.8	32.0	38.8**	55.3	17.9	72.6	37.4**	–17.3^{ns}	NC
UPRI 95-174	79.0	67.9	11.1^{ns}	73.5	30.7	77.3	42.8*	–03.8^{ns}	WC
	71.4	67.4	03.9^{ns}	69.4	18.5	72.2	50.8**	–20.7^{ns}	WC
UPRI 95-175	78.8	35.7	43.21**	57.3	30.7	77.3	26.6*	–20.0^{ns}	NC
	73.6	18.7	54.8**	46.1	18.5	72.2	27.6*	–26.0^{ns}	NC
UPRI 95-176	85.3	38.9	46.4**	66.7	33.8	77.7	32.9**	–10.9^{ns}	NC
	71.7	30.1	41.6**	55.0	17.9	72.6	37.1**	–17.5^{ns}	NC
UPRI 95-177	81.2	40.1	41.1*	60.6	29.4	77.1	31.2^{ns}	–16.4^{ns}	NC
	68.9	25.1	43.8**	48.2	16.7	73.1	31.5^{ns}	–24.8^{ns}	NC
Group mean	79.2	49.8	29.0						
	69.8	38.4	31.3						

* and ** Significant at 5 and 1% levels of significance, respectively, ^{ns} = non significant
WC = Wide compatible, IC = Intermediate compatible, NC = Narrow compatible,
I = Indica tester, J = Japonica tester

Table 2. Percent spikelet fertility of F_1 hybrids involving rice varieties of three varietal group with indica (I) and japonica (J) testers in field (light) and glasshouse (bold) environments at Hyderabad and Pantnagar, respectively

Varietal group/ variety	Mean spikelet fertility (%)								Compatibility group
	F_1 hybrid			Array mean	I × J F_1 mean	Tester parent mean	Difference from the array mean		
	I tester	J tester	Differences				I × J F_1 mean	Tester parent	
Aus (Group II)									
N 22	75.1	77.5	-02.4^{ns}	76.6	29.9	76.7	46.6^{**}	-00.1^{ns}	WC
	67.7	63.7	03.9^{ns}	65.7	12.8	72.7	52.9^{**}	-07.0^{ns}	WC
Dular	72.8	77.7	-04.9^{ns}	75.3	30.2	77.9	45.0^{**}	-02.6^{ns}	WC
	71.3	72.6	01.2^{ns}	72.0	20.0	72.9	51.9^{**}	-00.9^{ns}	WC
Group mean	74.0	77.6	-03.6						
	69.5	68.1	01.7						
Basmati (Group V)									
UPR 85-71-8	77.9	46.6	31.3^{**}	62.2	32.4	78.3	29.8^{*}	-16.0^{ns}	NC
	66.7	30.5	36.2^{*}	48.6	16.2	73.3	32.3^{ns}	-24.7^{ns}	NC
UPR 85-71-8-1	84.3	35.9	48.4^{*}	60.1	29.4	77.1	30.7^{ns}	-16.9^{ns}	NC
	65.6	17.6	48.0^{*}	41.6	16.7	73.1	24.8^{ns}	-31.5^{ns}	NC
Group mean	81.1	41.3	39.8						
	66.2	24.0	42.1						
Japonica (Group VI)									
CNTLR 80076-44-1-1-1	28.4	80.6	-52.1^{*}	54.5	29.4	77.1	25.1^{ns}	-22.5^{ns}	NC
	27.2	67.6	40.3^{**}	47.4	16.7	73.1	30.7^{ns}	-25.7^{ns}	NC
HUA LIEN YU 73	31.9	86.2	-54.2^{**}	53.6	28.2	86.7	25.4^{Ns}	-23.0^{ns}	NC
	37.5	77.3	39.7^{**}	53.4	16.9	72.4	36.4^{**}	-18.9^{ns}	NC
Moroberekan	80.8	75.0	05.5^{ns}	77.9	29.4	77.1	48.4^{**}	00.8^{ns}	WC
	72.9	67.2	05.7^{ns}	70.0	16.7	73.1	53.3^{**}	-03.0^{ns}	WC
Palawan	75.5	85.8	-10.3^{ns}	80.7	30.2	77.9	50.5^{**}	02.7^{ns}	WC
	65.8	72.0	06.2^{ns}	68.9	20.0	72.9	48.8^{**}	-04.0^{ns}	WC
Group mean	54.1	81.9	-27.8						
	50.9	71.0	-20.1						

* and ** significant at 5 and 1% levels of significance, respectively, ns = non significant, WC = Wide compatible, IC = Intermediate compatible, NC = Narrow compatible, I = Indica tester, J = Japonica tester

observed [12] at IRRI who grouped tropical japonica varieties Padi Bujang Pendek and Ketan Nagka into intermediate compatible group in the philippines while these were found to be wide compatible in Japan [4, 8]. Such a differential behaviour might be due to differences in screening conditions and the effect of diverse geographical conditions. Intervarietal F_1 spikelet sterility is also known to be affected by time of planting [1-2, 10] and differences in locations (16). The wide compatibility trait of Dular, N 22, Moroberekan and Palawan appear to be stable over environments. In order to identify stable WCVs, it would be useful to evaluate them over range of environmental conditions.

Table 3. Segregation of plants for spikelet fertility in three variety testcross progenies

Test cross progeny	Total population	Segregation of plants in F_1 progeny					χ^2 1:1
		Semisterile		Intermediate		Fertile	
RP 1579-1701-131-8/ Toyonishiki//IR 36	124	33	52	38	72	53	3.23^{ns}
RP 1579-1701-131-8/ IR 36//Toyonishiki	33	15	19.5	09	13.5	09	1.12^{ns}
UPR 1279-1-4-1/ Toyonishiki//IR 50	65	14	26.5	25	38.5	26	2.23^{ns}
UPR 1279-1-4-1/ IR 50//Toyonishiki	48	16	22	12	26	20	0.35^{ns}
Pusa 560-2-203-338/ Toyonishiki//IR 50	71	19	31	24	40	28	1.15^{ns}
Pusa 560-2-203-338/ IR 50//Toyonishiki	94	33	44.5	23	49.5	38	0.27^{ns}
UPRI 95-170/ Taichung 65//IR 50	45	14	22	16	23	15	0.04^{ns}
UPRI 95-170/ IR 50//Taichung 65	21	05	8.5	07	12.5	09	0.81^{ns}
UPRI 95-170/ Taichung 65//IR 36	43	17	23.5	13	19.5	13	0.40^{ns}

ns = Non-significant

Study indicated wide compatibility trait to be present into indica, aus and japonica varietal groups. However none of the basmati varieties had the WC trait. We confirmed the wide compatibility nature of aus and japonica varieties and reported for the first time eight elite indica lines in rice collection viz., RP 1579-1701-1318, RP 1967-20503-1241, UPR 1279-1-4-1, Pusa 560-2-203-338, Narendra 118, UPRI 95-169, UPRI 95-170 and UPRO 95-174 as the WCVs.

An examination of the ancestry of newly identified indica WCVs UPRI 95-169 (Dular/Narendra 1), UPRI 95-170 (Dular/Akashi) and UPRI 95-174 (N22/White Bagri//NDR 80) revealed variety Dular as the possible donor of WC gene in respect of varieties UPRI 95-169 and UPRI 95-170 and N 22 for UPRI 95-174. The remaining five indica WCVs identified appeared to have different source of their WC gene. Allelic relationship of these WC gene(s) with known genes in the literature is being investigated.

Nature of inheritance of wide compatibility

Nine paired three variety test cross progenies evaluated at Pantnagar under field conditions (Table 3) segregated for the spikelet fertility in the ratio of 1 fertile: 1 semisterile after the plants with the intermediate category were divided equally between the two classes to minimise the bias caused by other genetic and non genetic system(s) causing sterility. It suggested that the inheritance of wide compatibility trait in all these varieties is under the control of single dominant gene. Similar nature of inheritance has also been reported in intervarietal crosses using different varieties by previous workers [8, 12, 17-18]. Simple and dominant nature of inheritance for wide compatibility would enable easy incorporation into varieties. Incorporation of diverse neutral alleles into a breeding line should help solve the problem of hybrid sterility in the wide crosses.

Linkage relationships

Linkage of gene(s) controlling the wide compatibility trait and the morphological marker anthocyanin pigmentation in the apiculus (chromogen) was detected in various three way testcrosses. Highly significant differences in the fertility were found among three way testcrosses F_1 plants possessing the 'C^+' allele indicating linkage with the WC gene(s) from RP 1579-1701-1318, UPR1279-1-4-1 and Pusa 560-2-203-338 varieties (Table 4). For the six three way testcross progenies involving these WCVs, the *chi-square* values for the independent segregation of the WC gene and the chromogen (C^+) marker were significant and the mean recombination value between these two loci was 34.2% (Table 5). It indicated loose linkage between two loci affecting these traits. Reports in the literature however, vary indicating loose linkage with a recombination value of 31.8% between these loci [12] whereas the WC gene was found to be independent of gene C^+ in line T984 derived from indica/japonica hybrid (19). In contrast, reports also indicated tighter linkage with C.O. value of 3.9 to 5.6% in a cross involving japonica WCV, Ketan Nangka (8). It is quite possible as the genes in two WCVs are non-allelic and therefore, WC gene in Dular must be located at distant position on the same chromosome than Ketan Nangka studied by them where the two genes are present on the same chromosome but at a closer position.

Table 4. Linkage between spikelet fertility and anthocyanin pigmentation in apiculus of plants (marker gene) in three paired testcross progenies

S.No.	Test cross progenies	Marker genotype	Population size	Mean spikelet fertility %	t-test
1	(RP 1579-1701-131-8/	C^+C^-	64	62.3	**
	Toyonishiki//IR 36)	C^-C^-	60	51.8	
	(RP 1579-1701-131-8/	C^+C^-	16	56.3	*
	IR 36//Toyonishiki)	C^-C^-	17	42.6	
2	(UPR 1279-1-4-1/	C^+C^-	38	62.1	**
	Toyonishiki//IR 50)	C^-C^-	27	46.5	
	(UPR 1279-1-4-1/	C^+C^-	21	61.0	**
	IR 50//Toyonishiki)	C^-C^-	27	43.4	
3	(Pusa 560-2-203-338/	C^+C^-	37	57.1	*
	Toyonishiki//IR 50)	C^-C^-	34	46.1	
	(Pusa 560-2-203-338/	C^+C^-	48	60.6	**
	IR 50//Toyonishiki)	C^-C^-	46	48.9	

* and ** = Significant at 5 and 1 per cent levels, respectively

C^+C^- = heterozygous for chromogen gene with pigmented apiculus

C^-C^- = homozygous recessive for chromogen gene with no pigmentation in apiculus

The isozyme loci *Est-2, Amp-3* and *Pgi* were also known to be located on the same chromosome on which C^+ and WC gene(s) are located [12, 20]. It is therefore, considered desirable to determine the linkage relationship between WC loci and the isozyme loci assigned to linkage group I. A close linkage with some isozyme loci would facilitate screening of breeding population for the plants carrying WC gene at the seedling stage itself, in contrast to C^+ gene identified only at flowering through anthocyanin pigmentation in glume tips. Search for tighter linkage of this gene with DNA markers like RFLP and RAPD would be most desirable.

Table 5. Segregation pattern of WC gene with chromogen (C^+) loci in the three way testcrosses

Paired test cross	Genotypes obtained in three way cross F_1 progeny				Total plants	Observed chi-square values			Recombination (%)
	Non-crossovers		crossovers			W vs w 1:1	C vs c 1:1	WC:Wc:wC:wc 1 : 1 : 1 : 1	
	WC	WC	WC	WC					
Rp 1579-1701/131-8/ Toyonishiki//IR 36	42	35	29	18	124	2.61	0.13	7.71**	37.0
RP 1579-1701-131-8/ IR 36//Toyonishiki	14	8	8	3	33	3.66	0.03	3.88*	33.3
	56	43	37	21	157	3.14	0.08	5.80*	35.2
UPR 1279-1-4-1/ Toyonishiki//IR 50	22	21	17	5	65	2.60	1.86	8.88**	33.8
UPR 1279-1-4-1/ IR 50//Toyonishiki	20	13	8	7	48	1.33	0.75	6.29*	31.2
	42	34	25	12	113	1.97	1.31	7.59**	32.5
Pusa 560-2-203-338/ Toyonishiki//IR 50	25	19	18	9	71	3.16	0.13	4.05*	38.0
Pusa 560-2-203-338/ IR 50// Toyonishiki	36	28	20	10	94	3.44	0.04	13.06**	31.9
	61	47	38	19	165	3.30	0.09	8.56**	35.0

* and ** = significant at the 5 and 1% levels, respectively

Study revealed that the magnitude of compatibility varied in different varietal groups of the cultivated rice. WCVs with better agronomic performance like are expected to have higher breeding values as their use would enable exploitation of heterosis in intersubspecific crosses (8). Findings are of great significance in the indica breeding programme in particular as many of the newly identified WC lines belonged to indica group and combine the traits of modern varieties like semidwarf stature, good to moderate tillering, early to medium duration and good grain type and therefore, offer great potential in breeding.

REFERENCES

1. W. T. Butany, C. Gangadharan and M. V. S. Sastry. 1961. Present position of japonica-indica hybridization project and steps for its intensification. Proc Rice Res Works conf, Cuttack, 1935: 83-104. Indian council of Agric. Res., New Delhi
2. R. R. Jennings. 1966. Evaluation of partial sterility in indica × japonica rice hybrids. Tech Bull 5, International Rice Research Institute, Los Banos, Philippines
3. L. P. Yuan. 1994. Increasing yield potential in rice by exploitation of heterosis. *In*: (S. S. Virmani ed.) 1994 Hybrid rice technology: new developments and future prospects pp 1-6 Internatl Rice Res. Inst., Los Banos, Philippines
4. H. Terao and U. Midusima. 1939. Some considerations on the classification of *Oryza sativa* L. into subspecies. Jpn. J. Bot., **10**: 213-258.
5. T. Morinaga and H. Kuriyama. 1958. Intermediate type of rice in the subcontinent of India and Java. Jpn. J Breed., **7**: 253-259.
6. M. H. Heu. 1967. Studies on the growth duration and hybrid sterility in remote cross breeding of cultivated rice. J. Korean Soc. of Crop Sci., **4**: 31-71.
7. H. Ikehashi. 1982. Prospects for overcoming barrier in the utilization of indica-japonica crosses in rice breeding. Oryza., **19**: 69-77.
8. H. Ikehashi and H. Araki. 1984. Varietal screening of compatibility types revealed in F_1 fertility of distant crosses in rice. Jpn. J. Breed., **34**: 304-313.
9. H. Ikehashi and H. Araki. 1986. Genetics of F_1 sterility in remote crosses of rice. *In*: Rice Genetics, International Rice Research Institute. **11**: 119-130.
10. D. S. Athwal and S. S. Virmani. 1972. Cytoplasmic male sterility and hybrid breeding in rice. *In*: Rice Breeding, pp 615- 620. Annu. Rep., Int Rice Res Inst., Philippines (Los Banos).
11. J. C. Glaszmann. 1987. Isozymes and classification of Asian rice varieties. Theor. Appl. Genet., **74**: 21-30.
12. R. V. Vijaya Kumar and S. S. Virmani. 1992. Wide compatibility in rice (*Oryza sativa* L.). Euphytica., **64**: 71-80.
13. R. G. D. Steel and J. H. Torrie. 1960. Principles and procedures of statistics McGraw-Hill Book Company, Inc., London.
14. H. Oka. 1988. Origin of cultivated rice. Elsevier/Japan Sci. Soc. Press., Amsterdam/Tokyo pp 254

15. Y. B. Xu, J. J. Wang and Z. T. Shen. 1989. Screening *indica* and *japonica* varieties for wide compatibility. IRRN., **14**: 6-7.

16. S. Sampath. 1963. The significance of hybrid sterility in rice. Proc Symp Rice Genet. Cytogenet. 1963. Elsevier, Amsterdam, pp. 175-186.

17. L. J. Lou, C. S. Ying, Y. P. Wang and X. K. Wang. 1991. Sources and selection methods for universally compatible cultivars of rice. Crop Genetic resources., **1**: 14-15.

18. C. Lu and X. G. Pan. 1992. Inheritance of wide compatibility in rice cultivars 02428 and 8504. Chinese J. Rice Sci., **6**: 113-118.

19. X. D. Zhu, J. L. Wang, Z. M. Xiong and X. Q. Yan. 1994. Studies on wide compatibility for utilization of heterosis between *indica* and *japonica* rice. Chinese J. of Rice Sci., **8**: 211-216.

20. M. Nakagahara and K. Hayashi. 1976. Detection of esterase enzyme loci of *Oryza sativa* L.. Jpn. J. breed., **26** (suppl 1) : 114-115.