Genetic analysis of wide-compatibility trait in elite cultivars of indica rice, *Oryza sativa* L.

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ABSTRACT

Genetic enhancement for higher yield potential through the exploitation of diverse gene pool from the groups of cultivated rice, indica and japonica can be achieved through utilization of wide-compatible varieties which possess neutral allele S_5^n for normal spikelet fertility from intersubspecific hybrids. Inheritance and relationship with the marker gene in eight elite indica wide-compatible varieties viz., RP 1579-1701-1318, RP 1967-20503-1241, UPR 1279-1-4-1, Pusa 560-2-20-3-338, Narendra 118, UPRI 95-169, UPRI 95-170 and UPRI 95-174 were studied in 24 three-variety paired test crosses involving wide compatable variety WCV, indica and japonica testers. Inheritance of WC trait in ail the WCY's was controlled by a single gene with dominance of, wide-compatible over narrow-compatibility. The WC gene in seven of the WCV's revealed loose linkage with chromogen gene (C^+) for anthocyanin pigmentation in apiculus colour on chromosome 6, with mean recombination value of 33.72 %. In the variety Narendra 118, no such linkage was observed as the gene was independent of chromogen gene. The implications of these findings in hybrid and recombination breeding for rice improvement are discussed.

Key words: *Rice, intersubspecific crosses, wide-compatibility gene, inheritance, linkage*

Early efforts on exploitation of massive diversity existing in indica and japonica gene pools for plant type, grain quality, stress tolerance were limited in rice breeding due to hybrid sterility in wide crosses (Butany *et al.*, 1961; Jennings, 1966 and Yuan, 1994). An allelic interaction leading to hybrid sterility in rice was however reported by Ikehashi and Araki (1984) at the S_5 locus on chromosome 6, where, the indica and japonica varieties have S_5^i and S_5^j alleles, respectively and some javanicas have neutral allele S_5^n. The donor of S_5^n is called as wide-compatible variety (WCV). Most of the wide-compatible varieties used to overcome sterility of *indica- japonica* hybrids were reported from Japan and IRRI mostly in *aus* and *japonica* varieties (Ikehashi and Araki, 1986, 1987; Araki *et al.*, 1988, Luo *et al.*, 1990). Information on we gene for hybrid fertility in the elite and indigenous background of indica types is meagre. Pedigree analysis of eight newly identified indica WCV's (Dwivedi *et al.*, 1999) revealed different source of their wide-compatibility genes. Reports indicate that S_5^n can not completely overcome the problem of low seed set in indica-japonica hybrids (Ikehashi and Araki, 1987). Therefore, new WC genes, non allelic to S_5^n, assume significance in breeding inter-subspecific hybrids. It would therefore, be most desirable to understand the nature of inheritance of wide-compatibility trait in these indica WCV's prior to their utilization in rice improvement programme. The aim of the present investigation, was therefore, to study the nature of inheritance of wc trait in the indica WCV's and determine their linkage with suitable marker to facilitate easier selection.

MATERIALS AND METHODS

Material of the inheritance study comprised of 24 three variety paired test cross F_1 progenies derived from crossing eight WCV's with three (IR 36 as indica and Akihikari and Taichuag 65 as a japonica) testers, which were retest crossed with indica tester in case of hybrid progeny involving *japonica* tester and vice versa. Test cross progeny alongwith parental lines were evaluated in the main crop season at the Crop Research Centre of G.B. Pant University of Agriculture & Technology, Pantnagar. Twenty one day old seedlings grown in green house were transplanted in the field. Single seedling hill^{-1} was transplanted adopting a spacing of 20 cm between rows and 15 cm between plants. Plant population among various test crosses ranged between 16 to 214. Standard cultural practices for raising a healthy crop were adopted. At maturity, data on spikelet fertility of individual plants were recorded. Test crossed plants with spikelet fertility upto 40% were considered semi sterile and those above 65% were fertile. Frequency of plants falling in the intermediate' fertility group of 40-65% were equally divided between fertile and semi sterile classes to minimize the bias in classification caused by environmental (Athwal and Virmani, 1972) and other genetic sterility system(s) (Oka, 1964 and 1988).

The same three-way cross population was studied for determining linkage of the WC loci with chromogen C^+ loci for anthocyanin pigmentation of apiculus colour. A t-test of unequal variance (Steel and Torrie, 1980) was used to compare the significance of differences in the mean spike let fertilities of the marker genotypes compared to the contrasting genotypes in each of the three-variety paired test cross progenies. Linkage of WC and the marker gene was computed as the proportion of observed frequencies of phenotypic recombinants to the parental types. Independent assortment of the WC gene and marker gene was tested by calculating Chi-square values.

RESULTS AND DISCUSSION

Grouping of plants for spikelet fertility into fertile and sterile classes displayed segregation of spikelet fertility in the ratio of 1 fertile : 1 sterile in all the 24 paired three-variety test crosses involving eight indica WCV's analyzed (Table 1). The results suggested the inheritance of wide-compatibility trait in these WCV's to be under the control of single gene and wide-compatibility trait was dominant over narrow compatibility in the inter-subspecific hybrids. Similar mode of inheritance of WC trait in indica/japonica crosses have been reported (Ikehashi and Araki, 1986; Kumar and Virmani, 1988, 1992 and Dwivedi et al., 1996, 1999). However, a complex genetic basis of wide-compatibility involving additional hybrid sterility loci in WCV's 02428 and Dular have been reported (Liu *et al.*, 1997 and Wang *et al.*, 1998). Study of the distribution of spikelet fertility in these progenies did not reveal distinct fertile versus semisterile classes due to the presence of intermediate plants giving almost continuous variation. Presence of such plants in the range of 40-65 per cent of spikelet fertility may be due to factors like other genetic sterility systems (Oka, 1964, 1988), environmental factors (Athwal and Virmani, 1972), presence of minor genes (Qui-Zu-bai *et al.*, 1991; Lu and Pan, 1992; Van *et al.*, 1992; Yanagihara *et al.*, 1995).

The frequency and spikelet fertility percentage of marker genotypes C^+C^- (heterozygous plant with pigmented apiculus) and C^-C^- (homozygous plants with non-pigmented apiculus) in test cross progenies involving the indica WCV's were studied (Table 2). Results revealed significantly higher spike let fertility in marker genotypes with anthocyanin pigmentation in apiculus in test cross F_1 plants as compared to those without pigmentation indicating presence of linkage of WC gene(s) in all the crosses except indica WCV Narendra 118. In progeny involving WCV Narendra 118 no relationships of spikelet fertility with anthocyanin pigmentation in apiculus were however observed.

Segregation pattern of WC and C^+ (chromogen) loci in all the 14 test cross progenies revealed highly significant values of Chi-square for the expected segregation of plants in the ratio of 1 WC : 1 We : 1 WC : 1 we plants (Table 3). It suggested linkage of WC gene(s) with the C^+ marker and the location of hybrid fertility loci on chromosome 6. Intensity of linkage of the WC gene(s) with marker gene was also determined and mean value of33.72% with a range of30.70 to 35.90% (Table 3) for different indica WCV's was recorded.

Reports on location of wide-compatibility gene on chromosome 6 and precise position were variable indicating its loose linkage with chromosome marker (Dwivedi *et al.*, 1999) to tight linkage with C.O. value of 3.9 - 5.6% in WCV Ketan Nangka (Ikehashi and Araki, 1984) to independent assortment of two genes in WCV T 984 (Zhu *et al.*,1994).

Relative variation observed in recombination value between WC loci and the C^+ marker present in different crosses involving different WCV's was of smaller magnitude and are comparable to similar reports

Table 1. Segregation of plants for spikelet fertility in three-variety paired test crosses

Three variety	Total plants	Segregation of plants in F_1 progeny					$\chi^2(1:1)$
		Semi sterile	↔	Intermediate	↔	Fertile	
RP 1579-1701-1318/IR 36// Akihikari	214	87	115.5	57	98.5	70	1.36^{ns}
RP 1579-1701-1318/IR 36// Taichung 65	16	4	6	4	10	8	0.94^{ns}
RP 1579-1701-1318/ Akihikari//IR 36	53	244	30.4	12	23.0	17	0.94^{ns}
RP 1967-20503-1241/IR 36// Akihikari	197	90	109.0	38	88.0	69	2.26^{ns}
RP 1967-20503-1241/IR 36// Taichung 65	21	10	12.0	4	9.0	7	0.43^{ns}
RP 1967-20503-1241/ Akihikari//IR 36	64	32	37.5	11	26.5	21	1.95^{ns}
UPR 1279-1-4-1/IR 36// Akihikari	172	78	94.0	32	78.0	62	1.50^{ns}
UPR 1279-1-4-1/IR 36// Taichung 65	17	5	6.0	5	9.5	7	0.56^{ns}
UPR 1279-1-4-1/ Akihikari//IR 36	53	26	31.0	10	22.0	17	1.57^{ns}
Pusa 560-2-20-3-338/IR 36// Akihikari	205	91	115.0	48	90.0	66	3.10^{ns}
Pusa 560-2-20-3-338/IR 36// Taichung 65	34	8	13	10	21	16	1.88^{ns}
Pusa 560-2-20-3-338/ Akihikari//IR 36	84	37	46.5	19	37.5	28	0.98^{ns}
Narendra 118/IR 36// Akihikari	43	17	23.5	13	19.5	13	0.40^{ns}
Narendra 118/ IR 36// Taichung 65	40	12	18	12	22	16	0.40^{ns}
Narendra 118/ Akihikari//IR 36	33	15	19.5	9	13.5	9	1.12^{ns}
UPRI 95-169/IR 36// Akihikari	206	95	113.5	37	92.5	74	2.16^{ns}
UPRI 95-169/IR 36// Taichung 65	14	44	6	4	8	6	0.86^{ns}
UPRI 95-169/ Akihikari//IR 36	71	33	39.0	12	32.0	26	0.69^{ns}
UPRI 95-170/IR 36// Akihikari	210	99	116.0	34	94.0	77	2.33^{ns}
UPRI 95-170/IR 36// Taichung 65	18	5	7.5	5	9.5	8	0.50^{ns}
UPRI 95-170/ Akihikari//IR 36	60	29	35.0	12	25.0	19	1.71^{ns}
UPRI 95-174/IR 36// Akihikari	183	85	94.5	19	88.5	79	0.20^{ns}
UPRI 95-174/ IR 36// Taichung 65	21	7	9.5	5	12.5	10	0.41^{ns}
UPRI 95-174/ Akihikari//IR 36	59	30	36.5	13	22.5	16	3.52^{ns}

ns=non significant

in literature (Kumar and Virmani, 1992; Dwivedi *et al.*, 1999). Such variation may arise due to population size differences among test crosses used. There also exists the possibility that some minor and/or modifier genes might influence the expression of WC loci in plants at the border between sterility and fertility classes and it

Table 2. Linkage between spikelet fertility and anthocyanin pigmentation in apiculus (marker gene) of plants in three variety test cross progenies

Test cross progeny	Total number of plants	Marker genotype	Number of plants	Spikelet fertility (%)	t-test
RP 1579-1701-1318/IR 36// Akihikari	214	C^+C^-	112	60.1	**
		C^-C^-	102	41.5	
RP 1579-1701 -1318/ Akihikaril/IR 36	53	C^+C^-	25	55.2	**
		C^-C^-	28	39.9	
RP 1967-20503-1241/IR 36//Akihikari	197	C^+C^-	97	61.2	**
		C^-C^-	100	43.4	
RP 1967-20503-1241/ Akihikari//IR 36	64	C^+C^-	33	64.0	*
		C^-C^-	33	42.8	
UPR 1279-1-4-1/IR 36// Akihikari	172	C^+C^-	84	58.6	**
		C^-C^-	88	43.2	
UPR 1279-1-4-1/Akihikari//IR 36	53	C^+C^-	26	55.5	**
		C^-C^-	27	42.6	
Pusa 560-2-20-3-338/IR36//Akihikari	205	C^+C^-	99	60.6	**
		C^-C^-	106	47.4	
Pusa 560-2-20-3-338/Akihikari//IR 36	84	C^+C^-	37	56.2	**
		C^-C^-	47	44.1	
Narendra 118/IR 36//Akihikari	43	C^+C^-	22	64.1	ns
		C^-C^-	21	62.9	
Narendra 118/ Akihikaril/IR36	33	C^+C^-	17	61.4	ns
		C^-C^-	16	62.1	
UPRI 95-169/IR 36// Akihikari	206	C^+C^-	97	54.5	**
		C^-C^-	109	41.6	
UPRI 95-169/ Akihikari//IR36	71	C^+C^-	37	62.2	**
		C^-C^-	34	48.6	**
UPRI 95-170/IR 36//Akihikari	210	C^+C^-	107	60. 1	**
		C^-C^-	]03	44.6	
UPRI 95-170/Akihikaril/IR36	60	C^+C^-	26	55.8	**
		C^-C^-	34	49.2	
UPRI 95-174/IR36//Akihikari	183	C^+C^-	94	56.7	**
		C^-C^-	89	43.2	
UPRI 95-174/Akihikaril/IR36	59	C^+C^-	25	62.8	**
		C^-C^-	34	46.3	

may lead to misclassification of such plants.

The Chi-square values for independent segregation of WC and C^+ gene were non-significant in two of the crosses involving Narendra 118. Results from the present study have most explicitly shown that gene for wide-compatibility in Narendra 118 is independent of chromogen gene (C^+) on chromosome 6. It suggested that its WC loci was different from other seven indica WCV's analyzed as reported earlier (Zhu *et al.*, 1993). Ten different loci for hybrid sterility linked to C^+ or Wx marker on chromosome 6 have been reported (Kinoshita, 1993). Identification of new and diverse hybrid sterility loci on chromosome 6 would be of significance in hybrid breeding. Therefore, the necessity for study of very precise linkage between\VC loci and the tightly linked isozymic loci (Malik and Khush, 1995) or with molecular markers like RFLP (Zheng *et al.*, 1992) in newly evolved and elite indica WCV's was evident.

The results from the study have great significance due to single and dominant inheritance of the WC trait in exploitation of the WC genes for exploitation of intersubspecific heterosis utilizing two-line or three-line methods of hybrid breeding. Also, the

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Table 3. Segregation pattern of WC gene and chromogen (C^+) loci in the three variety paired test cross progenies

Paired test cross	Genotypes in F_1 progeny of three-way-cross				Number of plants	Observed χ^2 value			Recombination (%)
	Non cross over		Cross over			W vc w (1:1)	C vs C (1:1)	WC:Wc:wC:wc (1:1:1:1)	
	WC	wc	wC	Wc					
RP 1579-1701-1318/IR 36// Akihikari	68	72	44	30	214	1.510	0.467	21.07**	34.50
RP 1579-1701 -1318/ Akihikaril/IR 36	15	20	10	8	53	0.924	0.170	5.30*	34.00
	83	92	54	38	267	1.217	0.318	13.20**	34.25
RP 1967-20503-1241/IR 36//Akihikari	60	74	37	26	197	3.170	0.046	25.74**	32.00
RP 1967-20503-1241/ Akihikari//IR 36	18	22	15	9	64	1.560	0.060	4.27*	37.50
	78	96	52	35	261	2.370	0.050	156.0**	34.75
UPR 1279-1-4-1/IR 36// Akihikari	51	59	33	29	172	0.840	0.090	13.30**	36.10
UPR 1279-1-4-1/Akihikari//IR 36	15	19	11	8	53	0.930	0.020	4.25**	35.80
	66	78	44	37	225	0.890	0.055	8.789**	35.90
Pusa 560-2-21-3-338/IR36//Akihikari	59	75	40	31	105	3.050	0.240	19.18**	34.60
Pusa 560-2-21-3-338/Akihikari//IR 36	22	34	15	13	84	2.330	1.190	8.61**	33.30
	81	109	55	44	289	2.690	0.720	13.88**	34.00
Narendra 118/IR 36//Akihikari	12	7	10	14	43	1.880	0.023	0.55	55.81
Narendra 118/ Akihikaril/IR36	7	8	10	8	33	0.273	0.030	0.39	54.54
	19	15	20	22	76	1.076	0.026	0.47	55.18
UPRI 95-169/IR 36// Akihikari	63	80	34	29	206	2.350	0.720	30.50**	30.60
UPRI 95-169/ Akihikari//IR36	22	24	15	10	71	0.690	0.126	6.46*	35.20
	85	104	49	39	277	1.520	0.413	18.48**	32.90
UPRI 95-170/IR 36//Akihikari	70	74	37	29	210	0.690	0.080	29.20**	31.40
UPRI 95-170/Akihikaril/IR36	16	26	10	8	60	2.400	1.060	8.87**	30.00
	86	100	47	37	270	1.550	0.570	19.04**	30.70
UPRI 95-174/IR36//Akihikari	57	62	37	27	183	1.230	0.140	16.90**	35.00
UPRI 95-174/Akihikaril/IR36	14	25	11	9	59	2.860	1.370	6.72*	32.20
	71	87	48	36	242	2.045	0.760	11.81**	35.60

WC genes could be exploited in the recombination breeding utilizing diverse germplasm of indica and japonica cultivars in crosses for getting transgressive segregants in the segregating generations. Since the indica WCV's included are elite lines and combine several desirable characters of modern HYV's like medium tall to semi-dwarf stature, good to moderate tillering, early to medium duration and of good grain type. Exploitation of the WCV's offered a good diversity with respect to WC loci with greater choice by the plant breeder to select from the diverse pool. Since WC gene(s) was inherited as a dominant character it also suggested easier incorporation of the trait into genetic background of elite lines by simple backcrossing.

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