Research Article

Studies on wide compatibility in rice (*Oryza sativa* L.)

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Abstract :
The present investigation was carried out to screen different rice sub-species for wide compatibility (WC) and to evaluate F_2 populations of selected crosses to study the genetics of WC. Among the three criteria followed for screening of WCVs *viz.,* pollen fertility per cent of hybrids, spikelet fertility per cent of hybrids and the spikelet fertility per cent of hybrids as well as tester parents, the third criteria appeared to be effective. Based on spikelet fertility per cent of hybrids as well as tester parents, seven out of 15 lines *viz.,* Dular and ASD 16 (*indicas)*; WCR 6, IR 65600-32-4-6-1, IR 65601-120-3-5, IR 66158-38-3-2-1 and IR 67323-46-2-1 (tropical *japonica*) were adjudged as WCVs. The F_2 segregation in seven crosses for spikelet fertility and semi-sterility were in agreement with trigenic complementary ratio (45:19). Hence, it was concluded that the genetic basis of inter sub-specific sterility of cultivated rice is complex.

Key words:
Rice, Wide compatibility genes, F_1 hybrid sterility, inter sub-specific hybrids .

Introduction

The magnitude of heterosis depends on degree of genetic distinctiveness and combining ability of parental lines used. Hybridization between distantly related varieties has always been employed by plant breeders in crop improvement programmes. Usually, the inter sub-specific hybrids would be expected to be ideal cross combinations from viewpoints of adaptation and heterosis exploitation in crop improvement. However, heterosis for grain yield is difficult to realize because of high degree of spikelet sterility (Yuan, 1994), poor grain filling caused by lack of sink-source coordination and root senescence. Earlier studies indicated certain rice varieties to produce fertile F_1 hybrids when crossed with both *indica* and *japonica*s (Yuan, 1994). Significance of this phenomenon was recognized by Ikehashi (1982) who proposed to search varieties which can use for overcoming sterility barriers in *indica* / *japonica* crosses. Development of *indica* / *japonica* inter sub-specific hybrids. Therefore, it assumes greater significance in realizing higher magnitude of heterosis which is a prerequisite for wide spread adoption of hybrid rice technology. The *indica* / *japonica* hybrids were thought to be impossible 'until' the discovery of wide compatibility gene which overcomes the problem of F_1 hybrid sterility in such hybrids. This 'WC' gene has been incorporated into *japonica* kinds and successfully used for obtaining *indica* / *japonica* hybrids with higher levels of heterosis. The study of inheritance pattern of wide compatibility trait is as important as identifying the sources of WC genes. Identification of 'WC' gene sources becomes important either for its direct utilization in the development of inter sub-specific hybrids or for further use in rice breeding of parental lines with 'WC' genes. Progress in understanding the genetics of hybrid sterility has been slow because of its uniqueness. Therefore, it is necessary to screen and identify elite tropical *japonica* and *indica* genotypes possessing wide compatibility trait and its inheritance pattern for utilization in developing inter sub-specific hybrids.

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Material and methods

The experimental material includes all three sub species of rice *viz*., *indica*, *japonica* and tropical *japonica* (*javanica* / bulu varieties). Particulars of the materials are furnished (Table 1). Out of 21 genotypes, 15 (four *indica*s and 11 tropical *japonica*s) were used as 'lines' and six (three *indica*s and three *japonica*s) as 'testers' to get 90 cross combinations in 15 x 6 Line x Tester fashion. Control crosses were also made between *indica* and *japonica* testers whose spikelet fertility was used to screen wide compatibility (WC) based on method given by Vijayakumar and Virmani (1992). Wet cloth hybridization method devised by Chaisang, *et* *al*., (1967) was employed to generate crosses for study.

The 90 F_1s and 9 F_1s of control crosses along with their respective parents were raised with a inter and intra row spacing of 20 and 15 cm respectively in 3 The hybrids and parents were classified based on spikelet fertility also, as sterile (0 to 0.99 per cent), partial sterile (1 to 29.99 per cent), partial fertile (30 to 79.99 per cent) and fully fertile (80 to 100.00 per cent). Parents of F_1s showing more than 60 per cent pollen fertility were selected as good source of wide compatibility (WC) gene. A t- test of unequal variances was also used to screen the 'lines' as WC based on the spikelet fertility per cent (Steel. and Torrie, 1960). Classification of 'lines' into compatibility groups was done following Vijayakumar. and Virmani (1992). The 'lines' exhibiting mean hybrid spikelet fertility (array mean) significantly higher than that of the *indica*/*japonica* F_1 (mean data from control crosses), but also similar to 'tester' parent mean were designated as wide compatible varieties (WCVs). 'Lines' showing mean spikelet fertility of hybrid significantly higher than the mean of *indica*/ *japonica* F_1s, but significantly lower than the 'tester' parent mean were classified as intermediate compatible varieties (ICVs). 'Lines' realizing almost similar mean hybrid spikelet fertilities like that of *indica*/*japonica* F_1s, but significantly lower spikelet fertilities than the 'tester' parent mean were grouped as narrow compatible varieties (NCVs). To study the genetics of WC trait, the following seven hybrid combinations *viz.,* Dular x IET 16114, ASD 16 x IET 16920, WCR 6 x ASD 18, IR 65600-32-4-6-1 x ADT 43, IR 65601-120-3-5 x ADT 43, IR 67323-46-2-1 x ASD 18 and IR 66158-38-3-2-1 x ASD 18 were advanced to F_2 generation. The F_2 population of 200 plants of each cross were grown in a separate block along with corresponding parents on either side of the F_2's. Data were recorded on all the F_2 plants for spikelet fertility. The genetics of wide compatibility was analyzed based on the pattern of F_2 segregation. To divide the plants into different fertility groups based on spikelet fertility, the same scale already mentioned was followed.

Results and discussion

Screening genotypes for wide compatibility: While screening for wide compatibility (WC) genes, it is desirable to use atleast 4-5 'tester' genotypes to get reliable results (Vijayakumar *et al.,* 1999). Therefore, 15 genotypes (11 tropical *japonicas* and four *indica*s) have been selected as 'lines' and crossed with six 'testers' (three *indica* and three *japonica*). The results clearly showed that the pollen fertility per meter long row. All 20 F_1 plants in each combination and parents were scored for their pollen and spikelet fertility. Based on pollen fertility, the hybrids and parents were classified as sterile (0 to 0.99 per cent), partial sterile (1 to 29.99 per cent), partial fertile (30 to 59.99 per cent) and fertile (60 to 100.00 per cent). cent and spikelet fertility per cent of inter sub-specific hybrids vary extensively from partial sterile to complete fertile. Nine 'lines' showing more than 60.00 per cent mean pollen fertility per cent with all six testers, were screened as WCVs donors (Table 2). Similar yardstick for WC screening based on pollen fertility per cent was used by Ikehashi and Araki, 1984 and Govindaraj. and Virmani, 1988. Spikelet fertility studies of 90 F_1s also revealed that the same nine 'lines' recorded more than 80.00 per cent mean spikelet fertility with all the six 'testers', thus classified as fertile and wide compatible (Table 3). Vijayakumar and Virmani (1992), Kumar and Chakrabarti (2000) and Netaji (2002) followed similar scale for WC screening based on spikelet fertility per cent.

For confirmation of the above results a 't' test of unequal variances Steel and Torrie (1960), thereby classification of 'lines' into various compatibility groups *viz*., narrow compatible, intermediate compatible and wide compatible was also carried out (Dwivedi *et al.,*1999). The compatibility groups based on the spikelet fertility of hybrids as well as 'tester' parents revealed that seven out of nine 'lines' selected already were under 'WCV' group (Table 4). They were WCR 6, IR 65600-32-4-6-1, IR 65601-120-3-5, IR 66158-38-3-2-1, IR 67323-46-2-1 (all tropical *japonicas*), Dular and ASD 16 (*indica*s). Other four lines *viz.,* IR 20, N 22, IR 65597-17-7-3-3 and IR 68544-29-2-1-3-2 were classified as Intermediate Compatible Varieties (ICVs). The third group of NCV (Narrow Compatible Varieties) had four lines *viz.,* IR 66154-48-1-3-1, IR 66159-23-2-2-1, IR 66167-27-5-1-6 and IR 69353-70-3-1-1. Among the three criteria used for screening of wide compatibility *viz*., based on pollen fertility per cent of hybrids, spikelet fertility per cent of hybrids and spikelet fertility per cent of hybrids as well as 'tester' parents studied, the third criteria seems to be effective, since it is giving compatibility groups (i.e. WCV, NCV and ICV). Hence, the seven lines were identified as WCVs.

The present study revealed varied magnitude of compatibility in different varietal groups (*indica* / *japonica* / tropical *japonica*) of cultivated rice. WCVs with better agronomic performance would have higher breeding values as their use would enable exploitation of heterosis in inter sub-specific crosses (Ikehashi and Araki 1986 and Dwivedi, *et al.,*1999). Present findings are of greater significance in the tropical *japonica* breeding programme in particular, as many of the newly identified WC lines belonged to tropical *japonica* group and combined the traits of recent varieties like semi dwarf, good to moderate tillering, early to medium duration and good grain type and therefore, offer great potential in hybrid rice breeding.

The *indica* WCV *viz.,* Dular is expected to contribute to the heterosis breeding programme, especially in *indica* / *japonica* cross breeding by means of its broad compatibility of overcoming sterility problems in many remote crosses. Dular was reported as WCV by Vijayakumar and Virmani (1992); Dwivedi *et al.,* (1999); Vijayakumar *et al*. (1999) and Netaji (2002). The spikelet fertility performance of other six screened 'lines' were comparable with that of already proven WCV, *viz.,* Dular, confirming the six lines as WCVs. Similar type of screening based on proven WCVs was also reported by Kumar and Chakrabarti (1999) and Vijayakumar *et al*. (1999). ASD 16, another *indica* local high yielding variety fell under WC category. It is imperative to utilize this line in heterosis breeding to develop new high yielding hybrids with local preference.

Finally, it was concluded that the method for screening of WC based on spikelet fertility per cent of hybrids as well as 'tester' parents seems to be effective. Thereby, seven lines (two *indica*s *viz.,* Dular and ASD 16 and five tropical *japonica*s *viz.,* WCR 6, IR 65600-32-4-6-1, IR 65601-120-3-5, IR 66158-38-3-2-1, and IR 67323-46-2-1 were identified as WCVs. For further confirmation, it is suggested that these seven 'WC' lines identified may be subjected to molecular studies for tagging gene(s) related to WC trait.

Genetics of wide compatibility

The F_2 plants showed varied levels of spikelet fertility. For the analysis of F_2 segregation test, highly fertile class and fertile class were merged and designated as fertile class to minimize the bias caused by other genetic and non genetic systems causing hybrid sterility (Table 5). The other class is semi-sterile. The data on spikelet fertility for all the six crosses were subjected to Chi-square test for 3:1 probable ratio, based on the previous reports. Early workers suggested control of WC trait by single dominant gene fitting 3:1 ratio in Dular (Ikehashi and Araki**,** 1986., Vijayakumar and Virmani**,** 1988 and Vijayakumar and Virmani**,** 1992) and several other WCVs (Dwivedi *et al.***,** 1999). However, the present data does not fit into the 3:1 ratio. This shows the complex nature of inheritance of fertility in these seven crosses. These results are in agreement with Cheng and Xiang (1992) and Prabavathi (2000).

Whereas, after trying various combinations for goodness of fit in the above seven crosses, F_2 segregation for spikelet fertility and semi-sterility were in agreement with trigenic complementary ratio (45:19). The results are in consonance with that of Kumar and Chakrabarti (2000), Raghuram (2001) and Netaji (2002) who suggested involvement of non-allelic interaction in the expression of WC trait.

Based on the results of inheritance of WC trait, it may be suggested that, WC trait in above seven crosses is controlled by three genes (one basic dominant and two complementary genes) rather than single gene. Involvement of three genes rather than single gene in the expression of WC trait was also reported by Dwivedi *et al*. (1999) and Kumar and Chakrabarti (2000). Recently through RFLP analysis, three loci, one major and two minor genes, conferring significant effects on hybrid sterility have been identified (Liu et al., 1997).

The present study indicated complex genetic basis of spikelet fertility in inter sub-specific crosses. Further studies are necessary to fully characterize the genetic basis of WC genes in order to exploit the strong heterosis between *indica* and *japonica* or tropical *japonica* / *indica* varieties in hybrid rice breeding programme.

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Table 1. Details of parents used for crossing

Sl. No.	Genotypes	*Origin*	Group
Lines			
1.	Dular	India	*Indica*
2.	ASD 16	India	*Indica*
3.	IR 20	Philippines	*Indica*
4.	N-22	India	*Indica*
5.	WCR 6	Philippines	Tropical *japonica*
6.	IR 65597-17-4-3-3	Philippines	Tropical *japonica*
7.	IR 65600-32-4-6-1	Philippines	Tropical *japonica*
8.	IR 65601-120-3-5	Philippines	Tropical *japonica*
9.	IR 66154-48-1-3-1	Philippines	Tropical *japonica*
10.	IR 66158-38-3-2-1	Philippines	Tropical *japonica*
11.	IR 66159-23-2-2-1	Philippines	Tropical *japonica*
12.	IR 66167-27-5-1-6	Philippines	Tropical *japonica*
13.	IR 67323-46-2-1	Philippines	Tropical *japonica*
14.	IR 68544-29-2-1-3-1-2	Philippines	Tropical *japonica*
15.	IR 69853 -70-3-1-1	Philippines	Tropical *japonica*
Testers			
1.	MDU 5	India	*Indica*
2.	ASD 18	India	*Indica*
3.	ADT 43	India	*Indica*
4.	IET 16114	Japan	*Japonica*
5.	IET 16920	Japan	*Japonica*
6.	Odaebayeo	Japan	*Japonica*

Table 2. Pollen fertility per cent of F_1 hybrids in rice

Testers Lines	*Type*	MDU 5 (I)	ASD 18 (I)	ADT 43 (I)	Mean of three I testers	IET 16114 (J)	IET 16920 (J)	Odaebayeo (J)	Mean of three J testers	Mean of six testers
Dular	I	86.32	92.50	89.48	89.43	90.77	82.14	86.08	86.33	87.88
ASD 16	I	89.95	87.33	92.75	90.01	90.90	94.63	85.89	90.47	90.24
IR 20	I	93.58	86.75	92.22	90.85	61.36	62.15	68.81	64.11	77.48
N 22	I	70.60	71.32	73.50	71.81	64.72	64.06	66.42	65.07	68.44
WCR 6	TJ	83.13	92.88	85.28	87.10	85.42	87.50	92.90	88.61	87.86
IR 65597-17-7-3-3	TJ	15.26	55.02	58.68	42.99	55.71	58.26	53.33	55.77	49.38
IR 65600-32-4-6-1	TJ	93.78	87.73	91.97	91.16	85.46	90.58	92.55	89.53	90.35
IR 65601-120-3-5	TJ	85.04	88.47	94.68	89.40	81.27	85.50	83.25	83.34	86.37
IR 66154-48-1-3-1	TJ	55.00	54.61	55.46	55.02	51.87	55.65	27.91	45.14	50.08
IR 66158-38-3-2-1	TJ	86.73	87.28	80.86	84.96	81.79	84.90	86.85	84.51	84.74
IR 66159-23-2-2-1	TJ	40.00	33.63	51.67	41.77	59.78	52.15	33.73	48.55	45.16
IR 66167-27-5-1-6	TJ	59.51	59.78	56.07	58.45	43.82	46.32	37.71	42.62	50.54
IR 67323-46-2-1	TJ	80.40	85.77	84.28	83.48	89.15	82.17	84.02	85.11	84.30
IR 68544-29-2-1-3-2	TJ	29.65	45.08	35.64	36.79	47.32	48.10	45.78	47.07	41.93
IR 69353-70-3-1-1	TJ	8.18	32.65	34.14	24.99	36.74	56.39	19.09	37.41	31.20

I – *indica*, TJ – tropical *japonica*, J - *japonica*

Table 3. Spikelet fertility per cent of F_1 hybrids in rice

Testers / Lines	Type	MDU 5 (I)	ASD 18 (I)	ADT 43 (I)	Mean of three I testers	IET 16114 (J)	IET 16920 (J)	Odaebayeo (J)	Mean of three J testers	Mean of six testers
Dular	I	86.71	89.47	85.39	87.19	85.56	83.67	85.00	84.74	85.97
ASD 16	I	82.73	84.55	87.74	85.01	87.84	87.16	80.89	85.30	85.16
IR 20	I	89.95	87.33	92.75	90.01	90.90	94.63	85.89	90.47	90.24
N 22	I	89.32	87.65	92.13	89.70	90.12	92.35	88.67	90.38	90.04
WCR 6	TJ	86.67	82.02	86.15	84.95	83.83	86.01	87.39	85.74	85.35
IR 65597-17-7-3-3	TJ	53.65	52.35	51.17	52.39	54.87	53.64	55.92	54.81	53.60
IR 65600-32-4-6-1	TJ	83.82	85.28	80.13	83.08	80.10	90.06	82.54	84.23	83.66
IR 65601-120-3-5	TJ	87.50	83.96	87.38	86.28	80.40	81.11	88.28	83.26	84.77
IR 66154-48-1-3-1	TJ	36.04	37.04	54.38	42.49	40.65	23.58	29.58	31.27	36.88
IR 66158-38-3-2-1	TJ	80.38	84.20	85.72	83.43	88.91	82.59	80.17	83.89	83.66
IR 66159-23-2-2-1	TJ	50.46	51.32	49.76	50.51	62.22	61.62	63.15	62.33	56.42
IR 66167-27-5-1-6	TJ	67.21	18.17	75.29	53.56	52.47	56.24	16.01	41.57	47.57
IR 67323-46-2-1	TJ	83.30	85.08	80.08	82.82	80.47	90.00	82.57	84.35	83.59
IR 68544-29-2-1-3-2	TJ	48.32	54.45	51.25	51.34	62.32	54.24	58.75	58.44	54.89
IR 69353-70-3-1-1	TJ	40.21	29.34	19.18	29.58	71.32	40.26	64.71	58.76	44.17

I – *indica*, TJ – tropical *japonica*, J - *japonica*

Table 4. Spikelet fertility per cent of F_1 crosses with *indica* and *japonica* testers in rice

Designation	*Type*	Spikelet fertility (%)								Compatibility group
		F_1 hybrid mean			Array mean	I x J F_1 mean	Tester parent mean	Differences from the array mean		
		I tester	J tester	Differences				I x J F_1 mean	Tester parent mean	
Dular	I	87.19	84.74	2.45^{ns}	85.97	30.5	86.39	55.47*	-0.42^{ns}	WCV
ASD 16	I	85.01	85.30	-0.95^{ns}	85.16	30.5	86.39	54.99*	-0.90^{ns}	**WCV**
IR 20	I	90.01	90.47	-0.46^{ns}	90.24	30.5	86.39	59.74*	3.85*	ICV
N 22	I	89.70	90.38	-0.68^{ns}	90.04	30.5	86.39	59.54*	3.65*	ICV
WCR 6	TJ	84.95	85.74	-0.79^{ns}	85.35	30.5	86.39	54.85*	-1.04^{ns}	WCV
IR 65597-17-7-3-3	TJ	52.39	54.81	-2.42^{ns}	53.70	30.5	86.39	23.20*	-32.69*	ICV
IR 65600-32-4-6-1	TJ	83.08	84.23	-1.15^{ns}	83.66	30.5	86.39	53.16*	-2.73^{ns}	WCV
IR 65601-120-3-5	TJ	86.28	83.26	3.02^{ns}	84.77	30.5	86.39	54.27*	-1.62^{ns}	WCV
IR 66154-48-1-3-1	TJ	42.49	31.27	11.22^{ns}	36.88	30.5	86.39	6.38^{ns}	-35.85*	NCV
IR 66158-38-3-2-1	TJ	83.43	83.89	0.46^{ns}	83.67	30.5	86.39	53.17*	-2.72^{ns}	WCV
IR 66159-23-2-2-1	TJ	50.51	62.33	-11.82*	56.42	30.5	86.39	25.92*	-29.97*	NCV
IR 66167-27-5-1-6	TJ	53.56	41.57	11.99^{ns}	47.57	30.5	86.39	17.07^{ns}	-38.82*	NCV
IR 67323-46-2-1	TJ	82.82	84.45	-1.63^{ns}	83.64	30.5	86.39	53.14*	-2.75^{ns}	WCV
IR 68544-29-2-1-3-2	TJ	51.34	58.44	-7.1^{ns}	54.89	30.5	86.39	24.39*	-31.50*	ICV
IR 69353-70-3-1-1	TJ	29.58	58.76	-29.18^{ns}	44.17	30.5	86.39	13.67^{ns}	-42.22*	NCV

I – *indica*, TJ – tropical *japonica*, J - *japonica*

Table 5. Segregation for spikelet fertility per cent in F_2 generation of seven crosses in rice

Crosses	F_2 segregation				χ^2 45 : 19
	Fertile*				
	Highly fertile	Fertile	Highly fertile + Fertile	Semisterile	
Dular x IET 16114 (I x J)	106	53	159	41	2.09^{ns}
ASD 16 x IET 16920 (I x J)	102	55	157	43	1.25^{ns}
WCR 6 x ASD 18 (TJ x I)	56	90	146	54	0.45^{ns}
IR 65600-32-4-6-1 x ADT 43 (TJ x I)	62	86	148	52	0.12^{ns}
IR 65601-120-3-5 x ADT 43 (TJ x I)	60	87	147	53	0.27^{ns}
IR 66158-38-3-2 x ASD 18 (TJ x I)	52	93	145	55	0.71^{ns}
IR 67323-46-2-1 x ASD 18 (TJ x I)	55	94	149	51	0.04^{ns}
Expected ratio			**150.14**	**49.86**	

ns – Non significant, I – *indica,* TJ – Tropical *japonica*, J – *japonica*

* - The F_2 progenies of highly fertile and fertile classes were merged to single fertile class