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INHERITANCE OF REPRODUCTIVE STAGE COLD TOLERANCE AND ADAPTABILITY IN TWO *JAPONICA* × *INDICA* RICE CROSSES

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ABSTRACT

The inheritance of reproductive stage cold tolerance and adaptability was studied in seven generations of two japonica × indica rice crosses. Plants earmarked for cold treatment were subjected to low-temperature at 20°/15°C for 5 days in the naturally lighted 3-SAL cabinets in the phytotron at the International Rice Research Institute, Manila, Philippines at the first indication of panicle exsertion. The additive-dominance model was not a good fit for flowering duration, percent fertility and depression in percent fertility. Of the three epistatic effects, dominance × dominance and additive × additive types were more important. Complete to over-dominance was operative for the three characters. The narrow sense heritabilities ranged from 93% to 98%.

Key words : Rice, reproductive stage cold tolerance, gene effects, epistatic model

Great decrease in rice yields occur widely in cooler areas due to an abnormal increase in sterile spikelets. The sterile-type cool weather damage of rice plants induced by low temperatures during the booting and flowering stages results from unfertilized spikelets caused because of the indehiscence of anthers [1, 2]. The critical temperature for sterile-type cool weather injury has been reported to be 15° ± 5°C [3] and percent fertility and number of fertilized spikelets per panicle have been used as parameters for measuring cool weather injury at the reproductive growth stage in rice [4, 5].

Because of lack of efficient testing methods, reports on the mode of inheritance of reproductive stage cold tolerance in rice are few and far in between [6]. The study reported here was undertaken to determine the genetic architecture involved in the inheritance of characters associated with reproductive stage cold tolerance and adaptability in two japonica × indica rice crosses.

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MATERIALS AND METHODS

Screening for reproductive stage cold tolerance was based on seven generations (parents, F_1, F_2, B_1, B_2 and F_3) of each of the two japonica × indica rice crosses (Stejaree 45 × IR 9202 and Barkat × IR 9202) grown separately over time in 3 replications. The experiment was conducted in the phytotron of the International Rice Research Institute, Manila, Philippines.

Pregerminated seeds were sown in 5 × 5 cm plastic pots, one seed per pot, in the glasshouse under 25°/21°C temperature regime, 70/70 ± 1 relative humidity, and natural day length conditions. To facilitate production of uniform main culms, tillers were removed as they appeared. Each experiment accommodated both parents, one F_1, 10 F_2, 5 B_1 ($F_1 \times P_1$), 5 B_2 ($F_1 \times P_2$) and 30 F_3 rows, totalling to 53 rows per replication per cross. Each row had 34 uniform single-culm plants, half of which were earmarked at random for cold treatment and the other half left as control. Plants were subjected to cold treatment in the naturally lighted 3-SAL cabinets in the phytotron at 20°C from 0600 h to 1800 h and at 15°C from 1800 h to 0600 h for 5 days at the first indication of panicle exsertion. After expiry of the low-temperature treatment, the test cultures were allowed to mature under the glasshouse conditions at 25°/21°C. The panicles were harvested individually and the number of fertile and sterile spikelets counted. Percent fertility and depression in percent fertility were used as a measure of reproductive stage cold tolerance (the lower the depression, the greater the cold stability). Depression in fertility was worked out as the difference in fertility between low-temperature treated plants and control, expressed as a percentage of the control.

The weighted least square estimates of gene effects were estimated following the 3-parameter additive-dominance and 6- parameter epistatic model [7]. Heterosis was calculated as $[(h - i) - (d - j/2)]$ as per Jinks and Jones [8], narrow-sense heritability was calculated as per Allard [9] and inbreeding depression was worked out as $[(F_2 - F_1)/F_1 \times 100]$.

RESULTS AND DISCUSSION

The generation means, and estimates of heritability, heterosis and inbreeding depression are presented in Table 1. The estimates of gene effects are set out in Table 2.

For flowering duration, the F_1 was very close to the late (IR 9202) parent in the Stejaree 45 × IR 9202 cross and earlier to the early (Barkat) parent in the Barkat × IR 9202 cross, suggesting dominance of lateness in the former cross and earliness in the later cross. There was, however, a significant decline in heterotic effect in F_2

Table 1. Generation means and estimates of heritability (n.s.), heterosis and Inbreeding depression for three cold tolerance parameters in two rice crosses

Cross	Generation	Flowering duration	Fertility (%)	Depression in fertility (%)
Stejaree 45 × IR 9202				
	P_1	51.6 ± 0.1	78.7 ± 0.4	4.3 ± 0.5
	P_2	77.8 ± 0.1	51.7 ± 0.3	23.0 ± 0.4
	F_1	76.0 ± 0.1	39.9 ± 0.2	34.3 ± 0.5
	F_2	73.9 ± 0.1	47.1 ± 0.1	25.3 ± 0.1
	B_1	60.4 ± 0.1	61.9 ± 0.2	19.8 ± 0.2
	B_2	78.5 ± 0.1	43.5 ± 0.1	32.5 ± 0.1
	F_3	71.3 ± 0.1	44.7 ± 0.1	28.6 ± 0.2
Heritability (h_n^2)		95.3	97.9	98.6
Heterosis (%)		11.3**	–25.3**	20.7**
Inbreeding depression (%)		3.5**	–5.4**	1.4
Barkat × IR 9202				
	P_1	62.5 ± 0.1	63.6 ± 0.3	4.1 ± 0.7
	P_2	75.3 ± 0.2	43.8 ± 0.1	25.8 ± 0.3
	F_1	61.5 ± 0.1	40.0 ± 0.4	25.7 ± 0.3
	F_2	66.7 ± 0.1	43.3 ± 0.1	19.1 ± 0.5
	B_1	60.6 ± 0.2	52.1 ± 0.3	14.9 ± 0.3
	B_2	71.8 ± 0.1	43.2 ± 0.1	25.0 ± 0.1
	F_3	64.2 ± 0.1	44.6 ± 0.1	23.5 ± 0.2
Heritability (h_n^2)		93.2	98.0	98.3
Heterosis (%)		–7.4**	–13.7**	10.8**
Inbreeding depression (%)		1.5**	–3.5**	–1.2

n.s. : narrow sense

and F_3 due to inbreeding depression. The Barkat × IR 9202 hybrid demonstrated negative heterosis, leading to earliness, which is desirable for adaptability in low temperature areas. Higher mean value of F_2 than the F_1 in Barkat × IR 9202 was also suggestive of the presence of dominance and dominance interactions. Sohn *et. al.* [10] have reported partial dominance of early maturity over late maturity.

Significant negative heterosis for percent fertility was observed in both the crosses with the F_1 exceeding the lower parental limit in sterility. The mean F_2 and F_3 fertility was also nearer to the less fertile parent, suggesting lower fertility to be governed by dominant genes. Presence of dominance and epistatic gene effects was also indicated by higher F_2 mean values than F_1 mean values. A significant F_2 deviation from the average of F_1 and the mean parental performance in both the crosses indicated the presence of epistatic gene action [11].

The F_1 of the cross Stejaree 45 × IR 9202 demonstrated higher depression in percent fertility (lower cold tolerance) on account of low-temperature stress than the susceptible parent (IR 9202). F_1 was close to the susceptible parent (IR 9202) in Barkat × IR 9202 cross, suggesting partial to complete dominance of genes governing reproductive stage cold susceptibility. There was a general drop in depression in the F_2, F_3 and B_1 backcross generations. However, the depression in the B_2 backcross generation was very similar to that of F_1, indicating that most of the dominant genes for cold susceptibility have been contributed by the P_2 parent (IR 9202), resulting in higher depression (cold susceptibility) in the F_1 and B_2 generations. F_1 hybrids of both the crosses had greater depression than the mid- parental values, resulting in highly significant heterosis for the trait. The present results affirm that for imparting cold tolerance at the reproductive stage in rice, recessive genes governing resistance to cold susceptibility will have to be brought in a homozygous state. Expression of heterosis with respect to cold tolerance has earlier been reported by Sawada [2].

The Mather's [12] test for additivity indicated the significance of quantities A, B, C and D in most of the cases, revealing the presence of non-allelic interaction. The weighted least square analysis of the 6-parameter model [7] indicated the failure of the digenic model too for all the three characters in both the crosses (Table 2), suggesting the presence of higher order interactions or linkages or both.

The estimates of mean effects were positive and highly significant for the three characters in both the crosses. Both additive as well as dominant gene effects were highly significant in the inheritance of flowering duration, percent fertility and depression in percent fertility in both the crosses (Table 2). The magnitude of $\hat{h}$ was, however, more than that of $\hat{d}$ in most cases, indicating the preponderance of dominant gene effects. The parental lines, used in this study were highly selected for cold tolerance and high yield and this selection history was probably largely responsible for the low estimates of additive gene effects. The dominance effects for percent fertility and depression in fertility were positive for both the crosses which indicated dominance of gene effects in the inheritance of low- temperature induced spikelet sterility and depression in fertility. Importance of both additive and dominance gene effects for low-temperature induced spikelet sterility in rice has been reported [4, 5], with the major contribution coming from dominance effects [4]. Kaw and Khush [13] have shown percent fertility to be governed predominantly by additive gene action and depression in fertile spikelets and percent fertility predominantly by non-additive gene action.

Table 2. Estimates of gene effects on a six-parameter model for three characters in two rice crosses

Estimates of gene effects	Flowering duration		Fertility		Depression in fertility	
	Stejaree 45 × IR 9202	Barkat × IR 9202	Stejaree 45 × IR 9202	Barkat × IR 9202	Stejaree 45 × IR 9202	Barkat × IR 9202
(m)	82.6** ± 0.4	70.7** ± 0.5	42.8** ± 0.6	36.4** ± 0.9	10.3** ± 0.6	11.6** ± 2.2
(d)	−13.1** ± 0.1	−6.4** ± 0.1	13.5** ± 0.3	9.9** ± 0.2	−9.3** ± 0.4	−10.9** ± 0.4
(h)	−28.1** ± 1.1	−6.9** ± 1.4	20.1** ± 1.6	24.2** ± 2.4	36.2** ± 1.9	15.9** ± 4.8
(i)	−17.8** ± 0.3	−1.8** ± 0.5	22.4** ± 0.5	17.3** ± 0.9	3.4** ± 0.5	3.4 ± 2.2
(j)	−10.1** ± 0.4	−9.5** ± 0.5	9.9** ± 0.7	−1.9* ± 0.8	−6.6** ± 0.9	1.7 ± 1.0
(l)	21.6** ± 0.8	−2.3* ± 0.9	−23.0** ± 1.11	−20.6** ± 1.7	−12.2** ± 1.6	−1.8 ± 2.7
Chi-square (1 d.f.)	1177.8**	371.1**	38.3**	59.6**	934.6**	43.7**

Among the epistatic gene effects, dominance × dominance and additive × additive interactions were larger than additive × dominance interaction for flowering duration and percent fertility in the cross Stejaree 45 × IR 9202 and for percent fertility and depression in fertility in the cross Barkat × IR 9202. However, additive × dominance interactions were highly significant and of considerable magnitude for flowering duration in the cross Barkat × IR 9202 and for depression in fertility in the cross Stejaree 45 × IR 9202. Except for flowering duration in the cross Barkat × IR 9202, the predominant interactions involved were suggested to be of the duplicate type, because of the dissimilar signs of *h* and 1 (Table 2).

The comparative values of additive *d* and dominance *h* effects of genes in proportion to, the origin of scale *m* are presented in Table 3. For all the three characters, the dominance effects showed a marked increase in proportionate contribution under the epistatic model compared with the non-epistatic model, except for flowering duration in the cross Barkat × IR 9202. The additive effects showed increase in proportionate contribution under the epistatic model only for percent fertility in both the crosses and depression in fertility in the Barkat × IR 9202 cross.

Table 3. Comparative values of $\hat{d}$ and $\hat{h}$ under epistatic and non-epistatic models for three characters in two rice crosses

		Flowering duration		Fertility		Depression in fertility	
Estimate	Model	Stejaree 45 × IR 9202	Barkat × IR 9202	Stejaree 45 × IR 9202	Barkat × IR 9202	Stejaree 45 × IR 9202	Barkat × IR 9202
d/m	Epistatic	0.16	0.09	0.32	0.27	0.91	0.94
	Non-epistatic	0.21	0.12	0.22	0.16	0.93	0.71
h/m	Epistatic	0.34	0.10	0.47	0.67	3.53	1.37
	Non-epistatic	0.23	0.12	0.40	0.25	1.63	0.69
h/d	Epistatic	2.15	1.08	1.49	2.45	3.88	1.46
	Non-epistatic	1.08	1.01	1.78	1.54	1.75	0.97

The increase in the dominance component under the epistatic model could be attributed to the cancellation of opposing effects of digenic interactions as postulated under the duplicate type of epistasis.

The values of average dominance (*h*/*d*) in the non-epistatic model, indicated complete dominance of flowering duration in both crosses and depression in fertility in the Barkat × IR 9202 cross. For other cases overdominance was indicated. However, in the epistatic model, the average dominance ranked from complete dominance to over-dominance. Complete dominance was observed only for flowering duration in the Barkat × IR 9202 cross. The average dominance values may have been inflated because of the existence of different forms of epistasis. Toriyama and Futsuhara [14] have also reported cold tolerance to be nearly completely dominant.

In view of the significant additive effects for the three characters in both the crosses and high heritability estimates, ranging from 93.2% to 98.6% (because of uniform and favourable growing conditions in the glasshouse), it should be possible to select for an increased manifestation of reproductive stage cold tolerance in the material used. The additive × additive type of interaction effects, which were also considerable, may facilitate fixation of desirable combinations of genes. However, the large magnitude of *h* and the presence of duplicate epistasis in these traits would tend to hinder progress and make it difficult to fix them at a high level of manifestation. The selection should, therefore, be deferred until later generations when h effects would have diminished.

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