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Genetic Analysis of Growth Response to Cold Water Irrigation in Rice

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This study was carried out to obtain the basic information for breeding cold-tolerant rice varieties with high yield-productivity through wide crosses between indica and japonica rice. Genetic analysis was conducted using 55 F_1s obtained from half-diallel crosses among eleven cultivars of various origin including indica and japonica rice. Screening for cold tolerance was done with cold-water irrigation after transplantng until ripening stage. Both general combining ability (GCA) and specific combining ability (SCA) effects were highly significant in all characters associated with dry matter accumulation at 30 and 50 days after cold-water irrigation (DAC). The variance of GCA was much larger than that of SCA in plant height, shoot dry weight per plant (DWP), crop growth rate (CGR) and cold-water response index (CRI) of these characters except CRI of shoot dry weight per plant. The DWP, CGR and CRI of these characters of Gaochan 102, Tong88-7 and TR22183 were markedly higher than those of the others. GCA effects of these varieties on DWP, CGR and their CRI were also higher than those of the others, indicating that they are useful as promising parents for breeding cold-tolerant varieties. Analysis of genetic parameters for 11x11 half-diallel F_1s revealed that inter-locus gene interaction were concerned in the expression of plant height at 50 DAC, CRI of DWP at 50 DAC, and CRI of CGR, and that intra-locus gene interaction for plant height and the other characters were partial dominance and over-dominance, respectively. Narrow-sense heritability (h^2_N) was the highest in plant height as 0.729, and the lowest in CRI of DWP at 30 DAC as 0.048, suggesting that selection for cold tolerance will be quite effective in case that the selection criterion is the performance itself.

Key words : rice, cold tolerance, GCA, genetic parameters

Cold tolerance has been an important goal in rice breeding program in high-latitude countries such as Korea, Japan and north-eastern China, and in high-alpine area of tropical and subtropical countries. Up to date, the genetic analyses for the response of rice plants to cold-water irrigation have been conducted by many researchers. Futsuhara & Toriyama (1966) reported that cold tolerance was controlled by four major genes which were linked to d_2(II), *gh*(IV), *nl*(IX), and *bc*(XI), respectively. Sawada (1978) reported that spikelet sterility induced by cold temperature in F_2 showed continuous variation, and cold tolerance was linked to *Pr*(II), *Rc*(IV), *bc*(VI), and *Hg*(VII). Toriyama and Futsuhara (1960), Futsuhara and Toriyama (1971), and Moon and Rutger (1988) reported that selection for cold tolerance generally tended to increase culm length and panicle length, and to decrease panicle number. Several researches (Futsuhara and Toriyama, 1969, 1971; Jun and Yea, 1984; Kaw *et al.*, 1986. 1989; Nishimura and Hamamura, 1993; Sohn *et al.*, 1979; Toriyama and Futsuhara, 1960; Yea, 1995ab) have been conducted for analyzing the response of rice varieties to cold-water irrigation in agronomic characters at later growth stage such as days to heading, culm length, panicles per plant, spikelets per panicle, spikelet fertility etc., whereas few studies on cold response of growth characthers associated with dry matter production at early stage such as plant height, dry weight per plant, and crop growth rate etc.

The objective of this study was to obtain the genetic information on response of growth characters to cold water irrigation for breeding rice varieties with high cold tolerance and high yield productivity.

MATERIALS AND METHODS

The 55 F_1s were derived from half-diallel crosses among eleven rice cultivars including five japonica cultivars, Tong88-7, TR22183, Gaochan 102, Ilpumbyeo, and Dongjinbyeo, three tongil-type cultivars, Dasanbyeo, Milyang23, and Nonganbyeo which have high yield-productivity, and two NPT-type varieties from IRRI, IR66167-27-5-1-6 and IR66746-76-3-29 which have low-tillering and heavy-panicle

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plant architecture, and one indica type cultivar, China1039 which is known to have relatively high cold-tolerance in indica rice. Of them, Tong88-7, TR2183, and Gaochan 102 are introduced from Jilin, China as cold-tolerant varieties. The F_1s and parents were seeded on plastic-tunnel seed-bed of Seoul National University at Suwon on April 25, and the seedlings were transplanted in one plant per hill on the cold-tolerance screening nursery with the planting density of 25 x 15 cm at Chuncheon Sub-station of National Crop Experiment Station, Chuncheon, Korea in 1997. Field lay-out was followed by randomized complete block design with two replications. The fertilizer was applied at the rate of 12-8-8 kg/10a (N-P-K). Cold-water of 17°C was irrigated from 20 days after transplanting through the ripening stage.

Plant height and dry weight per plant at 30 (on July 14) and 50 (on August 3) days after cold-water irrigation (DAC) were investigated. Cold-water response index (CRI) were calculated as the ratio of performance in cold-water irrigation plot compared to the control plot. Shoot dry weight per plant was measured after drying the shoot samples, which were pulled out in whole plant and cut off all the roots, for five days in 80°C dry oven. Crop growth rate (CGR) was obtained by using the following formula: $CGR=(w_2-w_1)/(t_2-t_1)$ [g/m^2/days]. Where, w_2 and w_1 are the shoot dry weight per plant measured at 50 and 30 DAC, respectively. The t_2-t_1 corresponds to 20 days from 30 to 50 DAC.

Combining ability and genetic parameters were analyzed with model 2 (fixed model) of Griffing (1956) and Hayman (1954) methods.

RESULTS AND DISCUSSION

Response of parental varieties to cold-water irrigation

Plant height, shoot dry weight per plant (DWP), crop growth rate (CGR), and cold-water response index (CRI) of the characters of parental varieties at 30 and 50 days after cold-water irrigation (DAC) are shown in Table 1. Plant height, DWP, and CRI of the characters of Tong88-7, TR22183, Gaochan102 originated from Jilin province of China and China1039 under cold-water irrigation were markedly higher than those of the others. DWP and its CRI of Dongjinbyeo, CRI of DWP of Ilpumbyeo were relatively higher at 30 DAC, but significantly decreased at 50 DAC. CGR of Gaochan102, China1039, TR22183 and Tong88-7 were higher than those of others, while CRI of CGR of China1039 was much lower than that of above three japonica cultivars. Therefore, Tong88-7, Gaochan102 and TR22183 out of the parents were estimated as the most cold-tolerant varieties in viewpoint of dry-matter accumulation.

Combining ability analysis for growth characters under cold-water irrigation

Analysis of variance of general combining ability (GCA) and specific combining ability (SCA) for plant height, DWP, CGR and CRI of the characters under cold-water irrigation was shown in Table 2. All the GCA and SCA effects were significant. The variance of GCA effects were generally

Table 1. Varietal difference of plant height (PH) and shoot dry weight per plant (DWP) at 30 and 50 days after cold-water irrigation (DAC), crop growth rate (CGR) for 20 days during cold-water treatment between the above two stages and cold-water response index (CRI) of the characters in eleven parental varieties.

Parents	Varietal type	Origin	30 DAC				50 DAC				CGR	
			PH		DWP		PH		DWP			
			cm	CRI (%)	g	CRI (%)	cm	CRI (%)	g	CRI (%)	g/m^2/day	CRI (%)
Ilpumbyeo	Japonica	Korea	48.8	76.4	7.4	80.4	62.4	71.7	14.8	63.9	9.9	53.1
Dongjinbyeo	Japonica	Korea	54.3	74.9	9.5	78.5	68.5	76.5	14.7	63.2	6.9	46.5
Tong88-7	Japonica	Jilin	60.8	76.9	11.2	80.8	78.0	89.8	21.9	87.3	14.9	90.6
Gaochan102	Japonica	Jilin	68.3	88.1	13.2	82.7	85.6	92.3	26.4	86.8	18.8	86.2
TR22183	Japonica	Jilin	63.0	81.8	8.8	81.1	83.4	83.3	21.6	82.2	17.1	83.0
IR66167	NPT[a)]	IRRI	58.9	74.8	5.6	67.4	64.7	74.1	8.7	49.8	5.2	42.3
IR66746	NPT	IRRI	58.5	68.9	4.9	46.9	63.4	73.3	12.1	75.1	9.5	77.7
Nonganbyeo	Tongil	Korea	49.4	72.6	7.1	76.5	60.1	67.8	14.4	74.8	9.7	73.3
Dasanbyeo	Tongil	Korea	47.4	69.0	7.4	58.9	60.1	75.4	15.9	56.3	11.4	54.2
Milyang23	Tongil	Korea	49.8	74.5	7.6	60.9	69.4	71.4	15.9	66.3	11.2	61.7
China 1039	Indica	China	76.3	84.3	13.0	88.8	111.6	91.8	28.1	74.9	20.1	65.8

a) NPT: new plant type lines bred at IRRI.

Table 2. Mean squares of general combining ability (GCA) and specific combing ability (SCA) for plant height (PH), shoot dry-weight per plant (DWP) and crop growth rate (CGR) at 30 and 50 days after cold-water irrigation (DAC) and cold-water response index (CRI) of the charaters.

Item	Source	D.F.	30 DAC		50 DAC		CGR
			PH	DWP	PH	DWP	
Values[a)]	GCA	10	222.71**	10.37**	619.62**	68.52**	49.98**
	SCA	55	16.16**	3.25**	32.59**	10.39**	11.48**
	Error	65	1.93	0.40	5.43	1.61	4.58
CRI (%)	GCA	10	54.43**	20.16*	143.22**	97.18**	748.82**
	SCA	55	21.57**	119.78**	33.07**	133.78**	447.41**
	Error	65	5.28	9.54	7.25	4.68	104.36

a) Values: Performance at cold-water irrigation plot.
**,*: Significant at 1% and 5%, respectively.

Table 3. GCA effects of parents for plant height (PH), shoot dry-weight per plant (DWP) and crop growth rate (CGR) at 30 and 50 days after cold-water irrigation (DAC) and cold-water response index (CRI) of the characters in 11 × 11 half-diallel crosses.

Parents	30 DAC				50 DAC				CGR	
	PH		DWP		PH		DWP			
	cm	CRI (%)	g	CRI (%)	cm	CRI (%)	g	CRI (%)	g/m²/day	CRI (%)
Ilpumbyeo	-5.24	-2.18	-0.87	-1.15	-6.91	-2.47	-2.51	-0.68	-1.77	-4.27
Dongjinbyeo	-2.36	-2.20	-0.71	-0.02	-3.72	-2.24	-2.17	-2.22	-2.04	-9.86
Tong88-7	2.36	0.24	0.48	1.06	3.69	4.10	1.92	1.79	1.84	9.49
Gaochan102	3.44	2.24	1.34	0.90	10.05	6.89	4.49	4.32	4.11	13.78
TR22183	2.67	0.53	-0.01	1.05	5.68	1.19	0.81	0.23	1.51	2.62
IR66167-27-5-1-6	-0.09	4.00	-1.05	2.00	-6.25	0.36	-2.17	3.41	-1.59	3.98
IR66746-76-3-2	4.60	1.48	-0.88	-1.61	-3.20	0.80	-2.41	-1.85	-2.14	1.20
Nognanbyeo	-4.15	-0.89	-0.25	-0.02	-6.47	-5.31	-0.51	-0.97	0.44	-1.40
Dasanbyeo	-4.28	-2.79	0.27	0.21	-3.77	-0.97	0.32	-2.08	-0.03	-4.54
Milyang23	-3.59	-0.26	0.03	-0.33	-1.72	-1.78	-0.27	2.57	-0.50	0.55
China1039	6.64	-0.16	1.64	-2.09	12.64	-0.57	2.49	-4.51	1.05	-11.55

larger than that of SCA effects except in CRI of shoot dry weight per plant (DWP), indicating that variance components due to additive effects might be larger than those due to non-additive effects for these characters, although both additive and non-additive effects were important. Kaw *et al.* (1986, 1989) reported that leaf discoloration, days to heading, culm length, panicle length, spikelets per panicle, spikelet fertility under cold-water irrigation were mainly under the control of additive gene effects. Similar results were also reported by other reseachers (Futsuhara and Toriyama, 1971; Jun and Yea, 1984; Toriyama and Futsuhara, 1960).

The GCA of parental cultivars for growth characters was shown in Table 3. GCA effects of Gaochan102, Tong88-7 and TR22183 for plant height, DWP, CGR, and CRI of the characters under cold-water irrigation were relatively higher than those of the other parental varieties. In China1039, GCA effects were the highest for plant height and DWP, however, GCA effects for CRIs of the characters were very low indicating that the growth of F_1s derived from China1039-crosses in cold-water irrigation plot was greatly retarded as compared to the control. Consequently, it could be estimated that Gaochan102, Tong88-7 and TR22183 would be the promising parents for breeding cold-tolerant varieties in view of the biomass accumulation under cold-water irrigation.

Fig. 1 shows the relationship between GCA of parents for dry matter productivity in F1s and the parental performance. The GCA of parents for shoot dry-weight per plant and crop growth rate was positively correlated with the parental performance, indicating that the higher the parental value, the higher the GCA of the parent for the character in F_1. The GCA of parents for CGR and its CRI were also positively

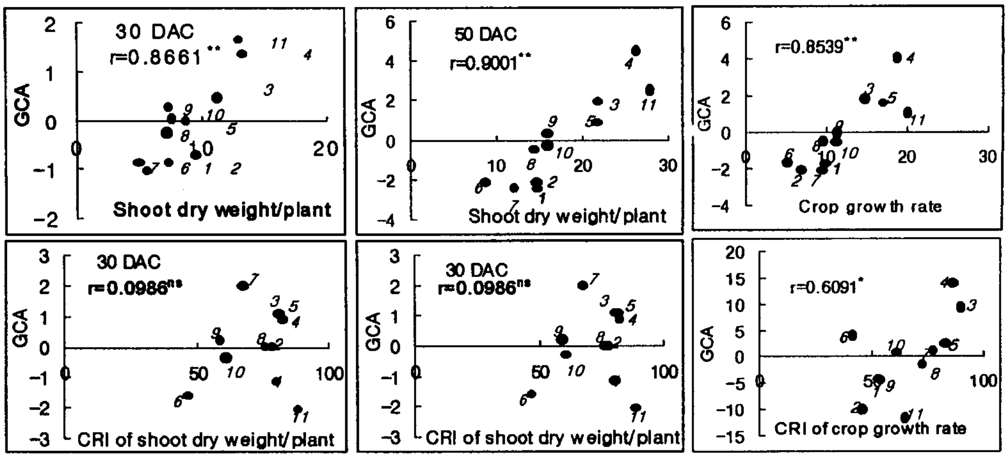

Fig. 1. Correlation coefficients between GCA effect and parental performance in shoot dry-weight per plant at 30 and 50 DAC and CGR under cold-water irrigation and in cold-water response index (CRI) of dry-weight per plant and CGR. (1. Ilpumbyeo, 2. Dongjinbyeo, 3. Tong88-7, 4. Gaochan102, 5. TR22183, 6. IR66167-27-5-1-6, 7. IR66746-76-3-2, 8. Nonganbyeo, 9. Dasanbyeo, 10. Milyang23, 11. China1039).

correlated with the parental performance. Meanwhile, GCA of parents for CRI of shoot dry-weight per plant was not correlated with parental performance. This agrees with the results of Table 2, implying that additive effect was relatively more important in DWP and CGR than non-additive effects, but less important in CRI of DWP. In addition, it seemed that indirect selection of F_1s having cold tolerance at early stage might be possible via parental performance of dry matter productivity at early stage under cold-water irrigation. Kaw *et al.* (1989) reported that GCA of parents for cold tolerance in F_1s was positively correlated with cold tolerance of parents. Nevado and Cross (1990) reported that GCA of parents for relative growth rate was positively correlated with GCA of parents for yield productivity in F_1s.

Analysis of genetic parameters

The Wr + Vr in all the characters except in CRI of plant height at 50 DAC were significant (Table 4), suggesting that dominant or multiplicative genetic variation existed for above characters. The Wr-Vr for plant height, CRI of shoot dry-weight per plant at 50 DAC and CRI of CGR were highly significant, indicating that the inter-locus gene interaction might be concerned in the expression of these characters. Regression coefficients of Wr on Vr for CRIs of plant height and shoot dry-weight per plant at 50 DAC and CRI of CGR showed significant difference from 1 by t-test (b=1), revealing that expression of the characters was governed by not only dominant variations, but also multiplicative genetic

Table 4. Significanct test of Wr + Vr or Wr − Vr array differences and t-test to intercept (a) and regrresion coefficient (b) of Vr. Wr linear regrression for cold-water response of plant height (PH) and shoot dry-weight per plant (DWP) at 30 and 50 days after cold water irrigation (DAC), CGR and cold-water response index (CRI) of the characters from 30 to 50 DAC in 11 x 11 half-diallel crosses.

Traits		Item	Wr+Vr	Wr − Vr	b	a	Significance in t-value		
							b=o	b=1	a=0
30 DAC	PH	Values[a)]	**	ns	0.809	10.05	**	ns	ns
		CRI	**	ns	0.791	-0.01	**	ns	ns
	DWP	Values	*	ns	1.009	-1.53	**	ns	ns
		CRI	**	ns	0.717	-71.42	**	ns	**
50 DAC	PH	Values	**	**	0.803	35.38	**	ns	*
		CRI	ns	ns	-0.104	0.00	ns	**	ns
	DWP	Values	**	ns	1.120	-2.24	**	ns	ns
		CRI	**	**	0.544	-73.12	**	**	**
CGR		Values	**	ns	0.781	-1.86	**	ns	ns
		CRI	**	**	-0.205	0.01	ns	**	ns

a) Values: Performance at cold-water irrigation plot.

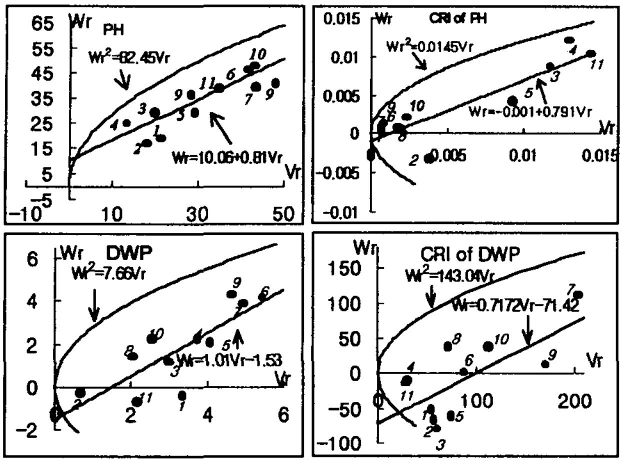

Fig. 2. Vr – Wr graphs for plant height (PH), shoot dry-weight per plant (DWP) at 30 DAC, and CRI of the characters in 11 × 11 half-diallel rice crosses (Refer to Fig. 1 for parental names).

variations among non-allelic genes. Similar results were reported for days to heading by Choi (1985). As the results of significant test on Wr + Vr, Wr – Vr, and regresson coefficients of Wr on Vr, plant height, shoot dry-weight per plant, and their CRI at 30 DAC, shoot dry-weight per plant at 50 DAC and CGR fitted to additive-dominance model which is applicable in case of no interaction among non-allelic genes.

The Wr – Vr graph were shown in Fig. 2 and Fig. 3. From the Figures, intra-locus gene interaction conferring plant height at 30 and 50 DAC seemed to be partial dominance with positive intercept. Overdominance gene interaction with significantly negative intercept (Table 4) was found in CRI of DWP at 30 and 50 DAC, and overdominance gene interaction which might be regarded as complete dominance gene interaction was found in CRI of plant height, DWP at 30 and 50 DAC, and CGR. The nearer to the point of the origin on the Vr-Wr graph a variety is located, the more it has dominant alleles (Hayman, 1954; Singh and Chaudhary, 1985). Gaochan102, Dongjinbyeo, Ilpumbyeo and Tong88-7 were located near to the origin on the Vr – Wr graph of plant height, indicating that these varieties possessed dominant alleles more than recessive alleles for the plant height. With the similar manner, it was inferred that Ilpumbyeo, IR66746-76-3-2, IR66167-27-5-1-6 and Nonganbyeo possessed more dominant alleles for the CRI of plant height, Dongjinbyeo, Nonganbyeo and China1039 possessed more dominant alleles for DWP, Gaochan102, China1039, Ilpumbyeo and Dongjinbyeo possessed more dominant alleles for the CRI of DWP, Nonganbyeo, Ilpumbyeo, Dongjinbyeo and Milyang23 possessed more dominant alleles for DWP at 50 DAC, and TR22183, IR66746-76-3-2 and Ilpumbyeo possessed more dominant alleles for the CGR.

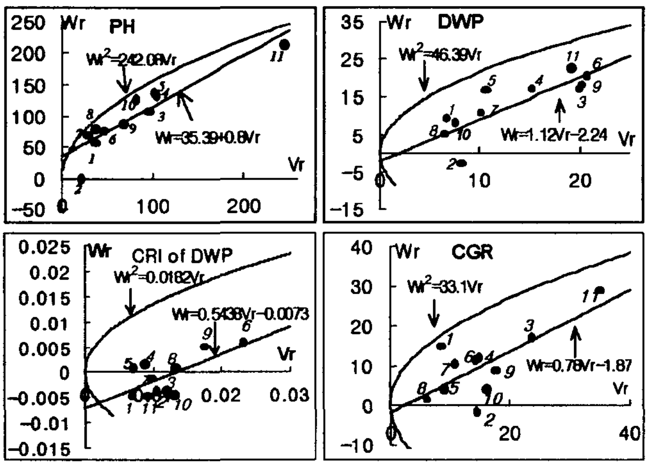

Fig. 3. Vr – Wr graphs for plant height (PH), shoot dry-weight per plant (DWP) at 50 DAC, CRI of DWP, and CGR in 11 × 11 half-diallel rice crosses (Refer to Fig. 1 for parental names).

Table 5 showed the genetic parameters for the characters estimated by Hayman's method (1954). The characters satisfying the assumptions made by Hayman were chosen in the Table. Average degree of dominance ($\sqrt{H_1/D}$) in intra-locus gene interaction for plant height at 30 days after cold water irrigation (DAC) was smaller than 1, indicating the partial dominance. Meanwhile, $\sqrt{H_1/D}$ of CRIs of plant height and DWP at 30 DAC, DWP at 50 DAC and CGR were larger than 1, suggesting the overdominance. This results agreed to Fig. 1 and Fig. 2. The $H_2/4H_1$ which represents the proportion of genes with posi-

Table 5. Genetic parameter estimates for plant height (PH), shoot dry-weight per plant (DWP), crop growth rate (CGR) and cold-water response index (CRI) of the characters under cold-water irrigation in 11 ×11 half-diallel crosses.

Genetic parameter	30 DAC				50 DAC	CGR
	PH		DWP			
	Values[a)]	CRI	Values	CRI	DWP	
D	79.60	0.0135	7.24	1.334	39.77	29.64
F	27.32	0.0137	7.32	3.073	37.99	24.25
H_1	58.48	0.0202	12.53	4.999	44.45	43.38
H_2	42.80	0.0135	9.65	0.317	33.08	35.23
$\sqrt{H_1/D}$	0.85	1.21	1.32	1.93	1.06	1.21
$H_2/4H_1$	0.18	0.17	0.19	0.16	0.19	0.20
k_D/k_R	1.50	2.40	2.25	3.93	2.64	2.02
$r_{(Wr+Vr,\ Yr)}$	-0.194	0.962	-0.528	-0.937	0.317	0.556
Gene No.	3.85	2.08	2.09	3.49	0.53	0.03
h^2_N	0.729	0.435	0.332	0.048	0.478	0.354
h^2_B	0.958	0.889	0.905	0.897	0.915	0.815

a) Values: Performance at cold-water irrigation plot.

tive and negative effects in the parents was nearly 0.25 for CGR, implying that the frequency of positive and negative alleles for CGR might be similar. The $H_2/4H_1$ for the other traits were smaller than 0.20, indicating that frequency of positive and negative alleles for the characters were unequal. The k_D/k_R which denotes the proportion of dominant and recessive alleles in the parents ranged from 1.50 to 3.93, indicating that frequency of dominance genes was higher than that of recessive genes. Estimated gene numbers varied along the characters. The DWP at 50 DAC and CGR were controlled by polygene, while plant height and its CRI at 30 DAC, DWP and its CRI at 30DAC were controlled by a few major genes. Narrow-sense heritability (h^2_N) was the highest in plant height as 0.729, and the lowest in CRI of DWP at 30 DAC as 0.048. The h^2_N for DWP was 0.332 at 30 DAC, however it was increased to 0.478 at 50 DAC. This was probably due to the fact that the differences in cold tolerance among genotypes were magnified by prolonged cold-water irrigation. This suggested that the selection for cold tolerance should be conducted at later stage. The h^2_N for performance of the characters at cold-water irrigation plot were much higher than those for CRI of the characters, indicating that genetic gain by selection for cold tolerance will be quite expected in case that the selection criterion is the performance itself.

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