Genetic Studies on Cool Tolerance in Rice

III. Linkage relations between genes controlling cool tolerance and marker genes of NAGAO and TAKAHASHI

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Synopsis. Cool tolerance was associated with the genes d_2 (linkage group II), gh (VI), nl (IX), and bc (XI), but not with the genes Rd (III), g and Rc (IV), la (VIII), and bl (X). The number of pairs of the genes controlling cool tolerance might be estimated as four or more.

Introduction

Numerous studies have been reported on the cool weather damages in rice. However, most of them have dealt chiefly with the physiological mechanism of the cool injury, while genetic studies are very few because the cool injury does not appear under the ordinary conditions and any efficient testing method of cool tolerance has not yet been established.

From such a point of view, the authors' investigations were directed primarily toward the establishment of the testing method on cool tolerance of a large number of bred lines (TORIYAMA 1962, FUTSUHARA and TORIYAMA 1964). Thus, the newly devised method which was named the improved method with cool water irrigation during the middle-growth stage, has made it possible to carry out a series of the experiments in relation to genetics and selection of cool tolerance (TORIYAMA and FUTSUHARA 1960, 1961). It was shown from those investigations that cool tolerance was determined by a few dominant genes, one of which showed linkage relation with the gene Pr (glume color localization), the other one with one of the gene An (awning).

The purpose of the present paper was to get further information on the inheritance of cool tolerance, through the linkage relations between the genes controlling cool tolerance and the marker genes of NAGAO and TAKAHASHI.

Materials and Methods

The marker genes of NAGAO and TAKAHASHI used in this investigation are listed in Table 1. According to NAGAO and TAKAHASHI (1963), each marker character behaves as a single gene to normal. Crosses were made in 1961 between each of the six linkage testers and Somewake which has the highest tolerance to cool among the Japanese varieties. F_1 plants of each cross were grown in the greenhouse in the winter, 1961-62 and F_2 populations were planted in the field under normal condition in 1962. In 1963, F_3 lines (five individuals per line) which were grown under systematic arrangement,

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Table 1. List of the testers and their marker genes (NAGAO and TAKAHASHI) used in this investigation

Tester	Marker gene (Linkage group)
A-5	<i>C</i> (I), <i>Pr</i> (II), <i>A</i> (III), <i>Rd</i> (III), <i>Rc</i> (IV), <i>I-Bf</i> (V)
H-9	<i>d₂</i> (II), <i>bc</i> (XI)
H-21	<i>Rc</i> (IV), <i>bl</i> (X)
H-25	<i>g</i> (IV), <i>la</i> (VIII)
H-69	<i>fs</i> (VII), <i>nl</i> (IX)
H-75	<i>Rc</i> (IV), <i>gh</i> (VI)

Table 2. Segregation of F_3 lines for the marker genes *Rc* and *Rd* in the cross A-5×Somewake

Item	Genotype			Total	χ^2	P
	<i>Rc Rd</i>	<i>Rc Rd⁺</i>	<i>Rc⁺ Rd</i> <i>Rc⁺ Rd⁺</i>			
Observed	24	5	7	36		
Expected*	20.25	6.75	9.00	36	1.58	0.50~0.20

* 9 : 3 : 4

Table 3. Relations between cool tolerance and the marker genes *Rc* and *Rd* in the cross A-5×Somewake

Genotype	Sterile index ($\sin^{-1} \sqrt{\%}$)								Total	Mean	Significance
	20	-30	-40	-50	-60	-70	-80	-90			
<i>Rc Rc</i> and <i>Rc Rc⁺</i>	1		7	9	7	1	4		29	58.32	N.S.
<i>Rc⁺ Rc⁺</i>			1	1	1	1	3		7	60.69	
<i>Rd Rd</i> and <i>Rd Rd⁺</i>	1		5	9	5		4		24	58.23	N.S.
<i>Rd⁺ Rd⁺</i>				2		2	1		5	58.60	

only the latter two genes were analysed in this investigation. According to NAGAO (1951), red pericarp was controlled by two complementary genes, *Rc* and *Rd*, *Rc* being responsible for production of the pigment, and *Rd* when it co-existed with *Rc*, responsible for spreading the color of *Rc*. *Rc* belongs to the linkage group IV and *Rd* to the linkage group III.

The segregation ratios of the F_3 lines concerning these genes are given in Table 2. The observed values were not depart significantly from the expectation. So the relations between these marker genes and cool tolerance were further examined and are shown in Table 3. There were no significant differences in cool tolerance among the genotypes for these marker characters.

2. Tester H-9×Somewake. The tester H-9 includes the two marker genes *d₂* and *bc*, of which the former belongs to the linkage group II, giving an ebisu dwarf, and the latter to the linkage group XI, a brittle culm.

The χ^2 test showed that the observed frequencies were not depart significantly from the expectation, although the frequency of the genotype *d₂⁺d₂⁺* was noted being rather higher than that of the genotype *d₂⁺d₂* (Table 4). Therefore, this discrepancy may be

together with their respective parents, were used for analysing their linkage relations. All F_3 lines and their parents had normal fertility under ordinary conditions, so the degree of cool tolerance was estimated from sterility observed under cool water irrigation and prior to analyses sterility percentages were transformed to angles as follows : sterile index = $\arcsin \sqrt{\%}$.

Results

1. Tester A-5 × Somewake. As shown in Table 1, the tester A-5 has the genes *C*, *A*, *Pr*, *I-Bf*, *Rc* and *Rd* as marker gene. However,

Table 4. Segregation of F_3 lines for the marker genes d_2 and bc in the cross H-9×Somewake

Item	Genotype									Total	χ^2	P
	$d_2^+ d_2^+$			$d_2^+ d_2$			$d_2 d_2$					
	$bc^+ bc^+$	$bc^+ bc$	$bc bc$	$bc^+ bc^+$	$bc^+ bc$	$bc bc$	$bc^+ bc^+$	$bc^+ bc$	$bc bc$			
Observed	3	5	0	2	2	1	1	1	1	16	10.50	0.50~0.20
Expected*	1	2	1	2	4	2	1	2	1	16		

* 1:2:1:2:4:2:1:2:1

Table 5. Relations between cool tolerance and the marker genes d_2 and bc in the cross H-9×Somewake

Genotype	Sterile index ($\sin^{-1} \sqrt{\%}$)								Total	Mean	Significance
	20	-30	-40	-50	-60	-70	-80	-90			
$d_2^+ d_2^+$	3	1			2	2			8	54.58	> *
$d_2^+ d_2$				1		3	1		5	73.76	
$d_2 d_2$						2	1		3	82.73	
$bc^+ bc^+$	1	1			1	3			6	62.08	N.S.
$bc^+ bc$	2				1	4	1		8	66.60	
$bc bc$				1			1		2	74.15	

* Significant at 5 % level.

attributed to the sampling error or the misclassification due to the small number of the tested lines and the plants within line.

Table 5 shows that the sterile index of the genotype $d_2 d_2$ was significantly higher than that of the genotype $d_2^+ d_2^+$, the genotype $d_2^+ d_2$ being between them with

Table 6. Segregation of F_3 individuals for the marker genes d_2 and bc and their relations with cool tolerance in the cross H-9×Somewake

Genotype	Observed	Expected*	χ^2	P	Sterile index	Significance
$d_2^+ d_2^+$ and $d_2^+ d_2$	57	50	2.61	0.20~0.10	61.19	> *
$d_2 d_2$	23	30			76.93	
$bc^+ bc^+$ and $bc^+ bc$	56	50	1.92	0.20~0.10	62.62	> *
$bc bc$	24	30			72.93	

† 5:3

* Significant at 5 % level

intermediate value. Similar relations were found among the genotypes $bc^+ bc^+$, $bc^+ bc$ and $bc bc$, although all differences did not show significance. However, the data were not adequate to determine the linkage relations owing to the small number of the F_3 lines tested, so the analysis was further carried out to find out whether there was any difference in cool tolerance among the genotypes on a per-plant basis. In spite of the fact that analysis of the data on a per-plant basis in F_3 is fraught with difficulty and uncertainty, the aforementioned relations could be also detected in this case (Table 6). The mere fact that the gene d_2 was associated with cool tolerance does not necessarily imply that the gene d_2^+ might be linked with the genes for cool tolerance, since phenotypic correlation between cool tolerance (sterile index) and stem length was -0.4193 and highly significant (TORIYAMA and FUTSUHARA 1961), and the gene d_2 is responsible for ebisu dwarf. However, the authors (1960) reported that cool tolerance was associated with the gene Pr located in the same linkage group (II) as the gene d_2 , and that the genes controlling cool tolerance behave independently of each other. Accordingly, it was suggested that one of the genes for cool tolerance was linked with the gene d_2^+ .

the other one with the gene bc^+ , respectively.

3. Tester H-21×Somewake. The tester H-21 has the two marker gene Rc and bl . The former is identical with Rc of the tester A-5, and the latter is the physiological disease gene showing dark brown discoloration of leaf and is located in the linkage group X.

As shown in Tables 7 and 8, analyses of the data gave a nonsignificant deviation from the expectation for the segregation ratios of these marker genes, and did not

Table 7. Segregation of F_3 lines for the marker genes bl and Rc in the cross H-21×Somewake

Item	Genotype										Total	χ^2	P	
	$bl^+ bl^+$				$bl^+ bl$				$bl bl$					
	$Rc Rc$	$Rc Rc^+$	$Rc^+ Rc^+$		$Rc Rc$	$Rc Rc^+$	$Rc^+ Rc^+$		$Rc Rc$	$Rc Rc^+$				$Rc^+ Rc^+$
Observed	2	6	2		3	6	2		3	5	1	33	8.23	0.50~0.20
Expected*	2.06	4.13	2.06		4.13	8.25	4.13		2.06	4.13	2.06	33		

* 1:2:1:2:4:2:1:2:1

show any significant difference in cool tolerance among the genotypes for these marker characters.

4. Tester H-25×Somewake. The tester H-25 has the genes la and g as marker gene. The gene la is located in the linkage group VIII, giving a lazy growth habit

Table 8. Relations between cool tolerance and the marker genes bl and Rc in the cross H-21×Somewake

Genotype	Sterile index ($\sin^{-1} \sqrt{\%}$)								Total	Mean	Significance
	20	30	40	50	60	70	80	90			
$bl^+ bl^+$				2	2	5	4	2	15	66.13	N.S.
$bl^+ bl$				2	3	3	3	1	12	63.45	
$bl bl$			1		2	2	3	2	10	65.48	
$Rc Rc$				1	3	3	3	1	11	65.16	N.S.
$Rc Rc^+$			1	1	3	6	5	1	17	63.06	
$Rc^+ Rc^+$				2		1	2		5	61.42	

Table 9. Segregation of F_3 lines for the marker genes g and la in the cross H-25×Somewake

Item	Genotype						Total	χ^2	P
	$g^+ g^+$		$g^+ g$		$g g$				
	$la^+ -$	$la la$	$la^+ -$	$la la$	$la^+ -$	$la la$			
Observed	41	15	66	26	28	14	190	4.24	0.95~0.50
Expected*	35.63	11.88	71.25	23.75	35.63	11.88	190		

* 3:1:6:2:3:1

and the gene g in the linkage group IV, a long empty glume.

As shown in Table 9, the segregation ratios of the F_3 lines provided a good fit to the expectation. Then, there were no significant differences in cool tolerance among the genotypes for these

Table 10. Relations between cool tolerance and the marker genes g and la in the cross H-25×Somewake

Genotype	Sterile index ($\sin^{-1} \sqrt{\%}$)								Total	Mean	Significance
	20	30	40	50	60	70	80	90			
$g^+ g^+$				7	6	17	13	13	56	68.08	N.S.
$g^+ g$			2	5	18	17	27	23	92	70.57	
$g g$				7	6	17	13	13	42	69.97	
$la^+ la^+, la^+ la$			2	10	19	37	38	29	135	70.13	N.S.
$la la$				3	12	11	14	15	55	70.45	

Table 11. Segregation of F_3 lines for the marker gene nl in the cross H-75×Somewake

Item	Genotype			Total	χ^2	P
	$nl^+ nl^+$	$nl^+ nl$	$nl nl$			
Observed	33	43	19	95	4.98	0.10~0.05
Expected*	23.75	47.50	23.75	95		

* 1:2:1

marker characters (Table 10).

5. Tester H-69×Somewake, The tester H-69 has the two marker genes nl and fs , but only the former gene was analysed in this investigation. The gene nl belongs to the linkage group IX, giving a neck leaf.

The χ^2 tests showed that the observed

Table 12. Relations between cool tolerance and the marker gene nl in the cross H-69×Somewake

Genotype	Sterile index ($\sin^{-1} \sqrt{\%}$)									Total	Mean	Significance
	10	-20	-30	-40	-50	-60	-70	-80	-90			
$nl^+ nl^+$		5	16	6	3	3				33	29.16	> *
$nl^+ nl$		8	18	10	4	1	1	1		43	30.16	
$nl nl$		1	4	9	1	3			1	19	37.99	

* Significant at 5% level

Table 13. Segregation of F_3 lines for the marker genes gh and Rc in the cross H-75×Somewake

Item	Genotype										Total	χ^2	P
	$gh^+ gh^+$			$gh^+ gh$			$gh gh$						
	$Rc Rc$	$Rc Rc^+$	$Rc^+ Rc^+$	$Rc Rc$	$Rc Rc^+$	$Rc^+ Rc^+$	$Rc Rc$	$Rc Rc^+$	$Rc^+ Rc^+$				
Observed	4	6	2	3	6	1	2	2	1	27	7.95	0.50~0.20	
Expected*	1.69	2.62	1.69	3.38	6.75	3.38	1.69	3.38	1.69	27			

* 1:2:1:2:4:2:1:2:1

Table 14. Relations between cool tolerance and the marker genes gh and Rc in the cross H-75×Somewake

Genotype	Sterile index ($\sin^{-1} \sqrt{\%}$)									Total	Mean	Significance
	10	-20	-30	-40	-50	-60	-70	-80	-90			
$gh^+ gh^+$		1	4	2	4	1				12	34.49	N.S.
$gh^+ gh$			1	4	3	2				10	40.04	
$gh gh$				2	2	1				5	43.12	
$Rc Rc$		1		3	5					9	37.62	N.S.
$Rc Rc^+$			4	4	2	4				14	38.79	
$Rc^+ Rc^+$			1	1	2					4	37.05	

frequencies did not depart significantly from the expectation, although the observed value of the genotype $nl^+ nl^+$ was somewhat larger than that of the genotype $nl nl$ (Table 11). While, a significant difference in cool tolerance was found between the genotypes $nl^+ nl^+$ and $nl nl$, and the genotype $nl^+ nl$ being between them with intermediate value. Consequently, one of the genes for cool tolerance appeared to be linked with the gene nl^+ (Table 12).

6. Tester H-75×Somewake. The tester H-75 has the two marker genes gh and Rc . The gene Rc is identical with that of the testers A-5 and H-21, and the gene gh belongs to the linkage group VI, giving a gold hull.

Table 15. Segregation of F_3 individuals for the marker genes gh and Rc and their relations with cool tolerance in the cross H-75×Somewake

Genotype	Observed	Expected*	χ^2	P	Sterile index	Significance
$gh^+ gh^+$ and $gh^+ gh$	92	84.38	1.84	0.20~0.10	35.90	> *
$gh gh$	43	50.63			43.16	
$Rc Rc$ and $Rc Rc^+$	91	84.38	1.39	0.50~0.20	39.19	N.S.
$Rc^+ Rc^+$	44	50.63			36.18	

† 5:3

* Significant at 5% level

The segregation ratios of the F_3 lines concerning these marker genes and their relations to cool tolerance are shown in Tables 13 and 14, respectively. It was found that the sterile index of the genotype $ghgh$ was higher than that of the genotype $gh^+ gh^+$, the genotype $gh^+ gh$ being between them, although not significantly. Also, a significant difference was found in the case of the observed values on a per-plant basis in F_3 (Table 15). On the other hand, there were no significant differences in cool tolerance among the genotypes $RcRc$, $Rc^+ Rc$ and $Rc^+ Rc^+$, being in accord with the results of the testers A-5 and H-21. From these results, it appeared that one of the genes for cool tolerance was linked with the gene gh^+ .

Discussion

Of twelve linkage groups corresponding to the haploid number of chromosomes in rice, eight linkage groups were analysed in this investigation. Besides, if tester and Somewake had the common gene for cool tolerance, such a gene was impossible to analyze. Therefore, it was not possible to obtain the complete information on the linkage relations for cool tolerance. It was suggested, however, that four of the eight linkage groups analysed, namely, II, VI, IX, XI each contain a different gene for cool tolerance.

In addition, further information could be obtained from the results of the authors' previous paper (1960). Cool tolerance was not associated with the chromogen gene for anthocyanin color, C , which is located in the linkage group I. Moreover, cool tolerance was associated with the gene Pr located in the same linkage group (II) as the gene d_2 , but not with the gene A located in the same linkage group (III) as the gene Rd . Accordingly, both tests gave the same results for their linkage relations. According to TAKAHASHI (1962), awning in rice is determined by three genes, each of which is included in the linkage groups VI, XI and XII. In the previous paper (1960), however, it was suggested that two genes should be responsible for awning in the variety Somewake, ones of them being linked with one of the genes for cool tolerance. If these two genes are assumed to be identical with two of three marker genes of TAKAHASHI, the one gene with the linkage relation would be considered to be located in either the linkage group VI or XI, while the other gene without the association in the linkage group XII.

To sum up, four of ten linkage groups were associated with cool tolerance (Table 16),

Table 16. Linkage relations between cool tolerance and the marker genes of NAGAO and TAKAHASHI

Linkage group	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Marker gene	<i>C*</i>	<i>d₂, Pr*</i>	<i>A*, Rd</i>	<i>g, Rc</i>		<i>gh</i>		<i>la</i>	<i>nl</i>	<i>bl</i>	<i>bc</i>	<i>(An)*</i>
Relation with cool tolerance	—	+, +	—, —	—, —		+		—	+	—	+	—

+, — indicate that cool tolerance is correlated or not with the marker gene, respectively.

* The results of the previous studies (1960).

suggesting that the number of linkage groups including the genes for cool tolerance might be estimated as four or more.

Subsequently, the theoretical frequency distributions were compared with the observed values to determine the validity of the genetic models postulated, using the data of F_2 , B_1 , B_2 , F_3 lines of the cross Somewake $\times$ Aomori No. 5 in the previous paper (1960). The theoretical values were computed from the estimated means and standard errors on the following assumptions: (1) cool tolerance is determined by five genes, (2) the parents are homozygous, one of them (Somewake) having all the dominant alleles and the other (Aomori No. 5) all the recessive alleles, (3) the genes act additively with the same effect, (4) tolerance is dominant to intolerance ($h/d=0.85$), (5) all gene pairs segregate independently. The standard errors of individuals were estimated from the envi-

Table 17. The estimated values of sterile index for each genotype computed on the assumption that the genes with the same effect act additively

No. of dominant genes	No. of dominant homozygotes					
	5	4	3	2	1	0
5	27.0 ¹⁾	28.7	30.5	32.2	34.0	35.7 ²⁾
4	38.6	40.3	42.1	43.8	45.6	
3	50.2	51.9	53.7	55.4		
2	61.8	63.5	65.3			
1	73.4	75.1				
0	85.0 ³⁾					

1) : Somewake type, 2) : F_1 type, 3) : Aomori No. 5 type, $h/d=0.85$

Fig. 1. Theoretical and observed frequency distributions of sterile index. Theoretical values were computed on the assumption that the genes with the same effect act additively. Solid line : Observed values
Broken line : Theoretical values

Table 18. Theoretical frequency distributions of sterile index for genotypes of F_2 , B_1 and B_2 computed on the assumption that cool tolerance is determined by five equivalent genes with $h/d=0.85$

No. of dominant genes	No. of dominant homozygotes	Frequency distributions of sterile index																	Frequencies†			
		Mean	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	F ₂	B ₁	B ₂
5	5	27.0	0.4	6.8	26.5	39.9	21.7	4.4	0.3											0.0010	0.03125	
	4	28.7	0.2	3.3	18.6	38.5	29.9	8.6	0.9											0.0098	0.15625	
	3	30.5		1.5	11.2	33.3	36.6	15.0	2.3	0.1										0.0391	0.31250	
	2	32.2		0.6	6.1	25.6	39.6	22.8	4.9	0.4										0.0782	0.31250	
	1	34.0		0.2	2.9	18.2	37.0	31.1	9.5	1.1										0.0782	0.15625	
	0	35.7		0.1	1.2	10.4	32.3	37.3	16.0	2.6	0.1									0.3013	0.30125	0.03125
4	4	38.6			0.2	3.5	19.0	38.7	29.4	8.3	0.9									0.0049		
	3	40.3			0.1	1.5	12.0	34.0	36.0	14.2	2.1	0.1								0.0391		
	2	42.1				0.6	6.3	26.1	39.6	22.3	4.7	0.4								0.1172		
	1	43.8				0.2	3.2	18.1	38.4	30.2	8.9	1.0								0.1563		
	0	45.6				0.1	1.3	10.7	32.7	37.1	15.5	2.5	0.1							0.0782		0.15625
3	3	50.2					0.1	1.5	12.4	34.4	35.7	13.8	2.0	0.1						0.0098		
	2	51.9						0.7	6.8	27.0	39.4	21.5	4.3	0.3						0.0586		
	1	53.7						0.2	3.3	18.6	38.5	29.9	8.6	0.9						0.1172		
	0	55.4						0.1	1.4	11.6	33.7	36.3	14.6	2.2	0.1					0.0782		0.31250
2	2	61.8							0.7	7.1	27.4	39.3	21.0	4.2	0.3					0.0098		
	1	63.5							0.2	3.6	19.5	38.9	28.9	8.1	0.8					0.0391		
	0	65.3							0.1	1.5	12.0	34.0	36.0	14.2	2.1	0.1				0.0391		0.31250
1	1	73.4									0.3	3.7	19.9	39.0	28.6	7.7	0.8			0.0049		
	0	75.1									0.1	1.7	12.7	34.7	35.4	13.4	2.0			0.0098		0.15625
0	0	85.0												0.1	1.8	13.0	35.1	50.0		0.0010		0.03125
F ₂	Calculated		0.00	0.16	1.39	5.66	10.65	14.39	17.49	16.06	13.32	0.50	5.70	3.26	1.45	0.62	0.21	0.07		100		5
	Observed			0.43	6.06	12.12	13.42	13.85	13.85	13.85	13.42	10.82	6.49	3.46	1.73	1.73	1.30	1.30	0		100	
B ₁	Calculated		0.04	1.42	9.63	38.84	35.95	19.32	4.38	0.40										100		
	Observed				3.45	44.83	34.48	10.34	6.90											100		
B ₂	Calculated			0.00	0.04	0.34	1.21	2.87	6.05	9.53	13.43	15.50	15.47	13.93	9.95	6.59	3.22	1.89		100		
	Observed					3.44	5.17	3.44	12.07	6.90	13.79	15.52	12.07	5.17	6.90	8.62	3.44	3.44		100		

† estimated from the following formulae

$$F_2 = \binom{5}{n} 2^{n-p} \binom{n}{n-p} / (2^5)^2$$

$$B_1 = \binom{5}{n} \binom{5}{p} / 2^5$$

$$B_2 = \binom{5}{n} \binom{5}{5} / 2^5$$

Where n =number of dominant genes, p =number of dominant homozygotes, S.E. =4.80

Table 19. Theoretical frequency distributions of sterile index for genotypes of F_3 lines computed on the assumption that cool tolerance is determined by five equivalent genes with $h/d=0.85$

No. of dominant genes	No. of dominant homozygotes	Frequency distributions of sterile index																		Frequency††
		Mean	V _E	V _G	S.E.†	20	25	30	35	40	45	50	55	60	65	70	75	80	85	
5	5	27.0	23.05	0	1.70	11.9	84.2	3.9												0.0010
	4	30.8	23.05	20.94	2.34	0.7	36.3	59.6	3.7											0.0098
	3	34.5	23.05	41.88	2.85		5.7	51.4	40.2	2.7										0.0391
	2	38.3	23.05	62.82	3.28		0.6	15.0	54.2	28.1										0.0782
	1	42.1	23.05	83.76	3.65			2.6	25.5	50.4	20.0	1.5								0.0782
	0	45.9	23.05	105.49	4.01			0.3	6.8	34.2	43.3	14.2								0.0313
4	4	38.6	23.05	0	1.70			1.7	77.7	20.6										0.0049
	3	42.4	23.05	20.94	2.34			0.1	15.1	71.5	13.2	0.1								0.0391
	2	46.1	23.05	41.88	2.85				1.6	33.2	56.7	8.4	0.1							0.1172
	1	49.9	23.05	62.82	3.28				0.1	6.7	44.4	42.7	6.0	0.1						0.1563
	0	53.7	23.05	83.76	3.65					0.9	14.7	48.5	31.7	4.1	0.1					0.0782
3	3	50.2	23.05	0	1.70					0.1	45.1	54.6	0.2							0.0098
	2	54.0	23.05	20.94	2.34						4.4	62.2	32.9	0.5						0.0586
	1	57.7	23.05	41.88	2.85						0.3	16.8	62.0	20.4	0.5					0.1172
												2.4	29.9	53.5	13.7	0.5				0.0782
	0	61.5	23.05	62.82	3.28															
2	2	61.8	23.05	0	1.70								14.5	82.5	3.0					0.0098
	1	65.6	23.05	20.94	2.34								0.8	38.9	57.3	3.0				0.0391
	0	69.3	23.05	41.88	2.85								0.1	6.5	53.3	37.8	2.3			0.0391
1	1	73.4	23.05	0	1.70										2.3	80.3	17.4			0.0049
	0	77.2	23.05	20.94	2.34										0.1	17.3	71.1	11.5		0.0098
0	0	85.0	23.05	0	1.70												0.1	49.9	50.0	0.0010
F ₃ line																				

†, †† estimated from the following formulae

$$S.E. = \sqrt{\frac{V_E + V_G}{m}}$$

where m = number of plants within line, V_E = environmental variance and V_G = genetic variance

$$F_3 \text{ line} = \binom{5}{n} 2^{5-p} \binom{n}{n-p} / (2^5)^2$$

where n = number of dominant genes and p = number of dominant homozygotes

ronmental effect and the standard errors of F_3 lines were estimated by adding the environmental variance and the corresponding genetic variance according to the genotype as shown in Tables 17, 18 and 19.

As shown in Fig. 1, the theoretical values in B_1 were in good agreement with the observed ones, whereas the theoretical values in F_2 , B_2 , F_3 lines tended to bias toward lower cool tolerance in comparison with the corresponding observed ones. The similar tendencies were observed in the cases of the assumptions in which cool tolerance was determined by four or six genes.

The above results indicate that some factors in the proposed models would not be fulfilled. Although no definite conclusion could be drawn with only the results of this investigation, it seemed unreasonable to assume that all the genes have the equivalent additive and dominant effects. However, this problem could not be accommodated also by either of the following two assumptions: (1) of the five genes controlling cool tolerance, the first three have twice the effect of the other two, or (2) the first three genes are completely dominant and the other two incompletely dominant.

Thereupon, the further assumption was proposed by taking into consideration of gene interaction. The item (3) of the first assumption was modified as follows: the

Table 20. The estimated values of sterile index for each genotype computed on the assumption that the gene action vary with the number of genes

No. of dominant genes	No. of dominant homozygotes					
	5	4	3	2	1	0
5	27.0	28.0	29.4	31.0	33.1	35.7
4	34.0	35.3	37.0	39.0	41.6	
3	42.7	44.4	46.4	49.0		
2	53.8	55.9	58.5			
1	67.6	70.2				
0	85.0					

Each sterile index was estimated from the exponential series $x\alpha^{5-n}$, where $x=27$, sterile index of Somewake and $x\alpha^5=85$, that of Aomori No. 5. $h/d=0.85$.

Fig. 2. Theoretical and observed frequency distributions of sterile index. Theoretical values were computed on the assumption that the gene action vary with the number of genes ($x\alpha^{5-n}$).

Solid line : Observed values
Broken line : Theoretical values

relation between the gene effects and the number of genes is shown by an exponential series $x\alpha^{5-n}$, where $x=27$, the sterile index of Somewake and $x\alpha^5=85$, that of Aomori No. 5. Thus, α was calculated to be 1.258. By using the values of x , α and $h/d=0.85$, the values of sterile index for each genotype were estimated as shown in Table 20 and Fig. 2. As the results, the theoretical frequency distributions were in fairly good agreement with the observed values in comparison with those of the first assumption, although there still were some discrepancies (Fig. 2).

These results indicate that the inherent mode of cool tolerance would be considerably complex, suggesting that further studies should be required in these respects.

Summary

Crosses between each of the six testers with the marker genes of NAGAO and TAKAHASHI and Somewake having the highest tolerance to cool were made in an attempt to clarify the linkage relations.

Each marker character behaves as a single gene to normal. The degree of cool tolerance was evaluated by sterile index ($\sin^{-1} \sqrt{\%}$) in the cool water irrigated field.

As the results, cool tolerance was associated with the genes d_2 (II), gh (VI), nl (IX) and bc (XI), but not with the genes Rd (III), g and Rc (IV), la (VIII) and bl (X). In addition, it was suggested from the authors' previous paper that cool tolerance was associated with the genes Pr (II) and one of the genes for awning (VI or XI), but not with the genes C (I), A (III) and the other one of the genes for awning (XIII). Therefore, the number of pairs of the genes controlling cool tolerance was estimated to be four or more.

The reliability of the genetic models postulated was discussed, particularly with reference to the frequency distributions, and it was suggested that the inherent mode of cool tolerance would be considerably complex.

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水稻における耐冷性の遺伝と選抜に関する研究

III. 長尾および高橋の標識遺伝子と耐冷性遺伝子との連鎖関係について

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水稻における耐冷性の遺伝機構を解明するため、耐冷性極強の染分と、長尾および高橋によつて作成された標識遺伝子を含む6つの検定親との間にそれぞれ検定交雑を行ない、各 F_3 系統について連鎖関係を調べた。

耐冷性遺伝子との間に連鎖関係の認められた標識遺伝子は、 d_2 , bc , nl および gh であり、これらはそれぞれ第 2, 11, 9, 6 連鎖群に含まれる。一方、相関関係の認められなかつた標識遺伝子は Rc , Rd , bl および g で、これらはそれぞれ第 3, 4, 10, 4 連鎖群に含まれる。なお、第1報の結果を併せ考慮した場合、第 1, 12 連鎖群はともに耐冷性遺伝子と相関関係はないものと推定されたので、これらの結果を総合すると、耐冷性遺伝子数と

して4コ以上が推定された。

一方、第1報で耐冷性の遺伝子分析に用いた染分×青森5号の F_2 , B_1 , B_2 および F_3 系統を用いて、耐冷性の遺伝子数を4~6コとし、単純に各遺伝子は同等の相加的な作用力を持ち、かつ優性度を0.85と仮定して理論分布を算出すると、 F_2 および F_3 の分布は実測値より耐冷性弱へ大きくずれた。そこで遺伝子の働きを加算的ではあるが保持する遺伝子数が増加するにつれて作用力が次第に頭打となる ($\alpha\alpha^{5-n}$) と仮定すると、実測値とかなりよく一致した。恐らく耐冷性の如き形質は遺伝子の働きが互に作用し合うような、かなり複雑な遺伝機構をもつものである。