いもち病抵抗性の遺伝 III

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Genetic Studies on Resistance of Rice Plant to Blast Fungus III. Decline in the blast resistance of Ginga, a descendant variety of Sensho

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後藤岩三郎：いもち病抵抗性の遺伝　Ⅲ．戦捷の
子孫品種銀河におけるいもち病抵抗性の低下

Abstracts

Lazy-Ginga, *la*-isogenic line of Ginga, proved that Rb_1 of Sensho linked with *la* had not been introduced to Ginga. Absence of Rb_1 caused a significant decline of blast resistance to Ginga. From comparison of derivatives with their common parent, Sensho, it was ascertained that the present decline commenced in the early stage of the breeding program.

The two blast resistance genes which controlled the moderate resistance of Ginga were assumed to be multiple alleles of the two ones other than Rb_1 of Sensho.

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Introduction

Since upland variety Sensho was employed as a female parent because of its high blast resistance, many useful lowland cultivars have been derived from the variety in these four decades, but all these descendants from crosses with Japanese lowland vars are more or less inferior in the blast resistance to the original parent. In this paper, Ginga was adopted as a tracer to pursue the process of decline of blast resistance in the breeding program.

Materials and Methods

According to the previous reports, the genealogical relationship of Sensho and its derivatives was [7,8,11] as follows : Sensho--Tasensho--Shinju--Futaba--Shuho--Ginga and Homare-Nishiki in order and the latter two were derived from the common parent, Shuho. "Ta" means a paddy field in Japanese, and Tasensho was inherent in many agronomic features of Japanese lowland vars other than in blast resistance[8]. Tasensho of intermediate parental line, Shinju and Futaba were raised 9,14 and 18 years after the program commenced. The writer's previous report[3] revealed that, the blast resistance of Sensho was controlled by three independent genes, Rb_1, Rb_2 and Rb_3, and the first one of major effect presented a recombination value of about 10% with *la*. The index-values of resistance were assumed for 27 genotypes of these genes on the basis of their cumulative effects.

Kamenoo and Norin 20 were selected as typical suscepible Japanese lowland cultivars. Two *la*-isogenic lines, lazy-Ginga and lazy-Kamenoo, were made available

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by the writer. Lazy-Ginga was selected from B_5F_4 of (H-79×Ginga)×Ginga and the other from B_6F_6 of (H-79×Kamenoo)×Kamenoo, and these were confirmed to be similar to respective recurrent parents in blast resistance. Other than *la*, *lg* was transferred to lazy-Ginga.

In addition to *la*, 8 marker genes of 6 testers were studied in linkage relationships between resistance genes of Ginga as noted in Table 6. These testers[9,13] were made available to the writer through the kindness of Dr. M. Takahashi of Hokkaido University.

Japan Race Group was adopted to classify each isolate after Kozaka *et al*[12].

In Exp. A, clay cups of ca. 50 cm^2 and 10 cm deep filled with sand were used to raise seedlings. Fertilizers given to each cup were 0.5 g of ammonium sulfate, 0.1 g of potassium chloride and 0.5 g of natrium diphosphate. Four plants were raised in each of 7 cups, which were alloted to each of 7 varieties and 5 of all the plants were inocultated with each isolate. Seedlings in Exp. B were raised in trays of 10 dm^2 and 5 cm deep, filled with sand and fertilized with 1.0 g of ammonium sulfate, 0.5 g of potassium chloride and 0.5 g of natrium diphosphate, seedlings planted in each tray being 40 in number. Two nitrogenous levels, high and low, were set up by top dressing of different amounts of ammonium sulfate, 5 g and 2 g, respectively. Five plants were assigned to each experimental plot. In the other experiments, materials were raised in trays of ca. 90 dm^2 and 15 cm deep and used according to the procedures previously reported[3,6].

The degree of resistance was assessed by the sheath inoculation method, and H. D. values were estimated in all the experiments except in Exp. A and in Exp. B, in which D values indicated more precise difference among the materials. In each of the 4 trays used in Exp. C, one set of 220 plants were raised in a glass house. The materials consisted of parental vars and progenies of 3 crosses, Sensho X lazy-Ginga, Sensho × lazy-Kamenoo and Ginga × Kamenoo. Two isolates, Ken 53-33 and Hoku 2, were doubly inoculated. Inoculation was given to one set a day and was finished in 4 days and these 4 data were totalized in one datum because of their similarity in reaction of parental vars and in segregation of resistance in F_2 plants. Exp. D-1 was conducted with 3 trays according to the same procedures of Exp. C, but in a different year and with different combination of isolates, Ken 53-33 and Hoku 1. The materials consited of progenies of Sensho × lazy-Ginga, parental vars and their related ones.

Three data of the present inoculation were put together in one for the same reason as that of Exp. C. Exp. D-1 was followed by Exp. D-2, in which F_3 lines raised from susceptible and normal F_2 plants and represented by about 25 seedlings were inoculated with Ken 53-33 and Hoku 2.

Exp. E was conducted under more susceptible conditions than under those of Exp. C and Exp. D, to observe increased number of susceptible plants in F_2 population of Sensho × Ginga. In Exp. F, pedegrees of Ginga × H-79 were inoculated with Hoku 2 in order to look for linkage relationships between resistance genes and marker genes of H-79. Next, resistance to Hoku 2 was traced as to F_3 lines of susceptible F_2 plants. A part of F_2 plants were doubly inoculated with Ken 54-04 and Hoku 2. In Exp. H, F_2 populations of each crosse of Ginga × testers were inoculated with Hoku 2 to observe segregation of resistance as well as of marker genes.

In each genic analysis of Sensho, genotypes were divided into two groups as to each isolate according to the index-values, resistance and susceptible, to correspond with the ratio of the former to the latter given in experimental datum[3].

Results

Level of blast resistance Ginga showed

The level of blast resistance Ginga showed was intermediate between Sensho and Japanese vars tested as in Tables 1 and 2. But the difference in D value between Ginga and other vars varied in degree with isolates, nitrogenous levels and leaf orders, and in some cases it became indistinguishable, (cf. the difference from Sensho in reaction to Naga 143 and in the 3rd leaf order and the difference from susceptible vars in reaction to Hoku 1 and in the 1st leaf order). Lazy-Ginga and lazy-Kamenoo were ascertained to be on similar level to the respective recurrent parents in blast resistance.

From the above-mentioned results it is very reasonable that segregation of pedegree in blast resistance was liable to vary according to many factors, and so *la* was a useful marker gene in the present analysis.

Table 1. Blast resistance of three varieties to five isolates

Item of Exp. a)	Isolate	Japan Race Group	D values of vars		
			Sensho	Ginga	Norin 20
A	Ken 53-33	T-1	1.0	1.3	4.5
	Naga 143	T b)	1.0	1.0	1.9
	Naga 89	C-3	1.0	1.2	3.7
	Hoku 1	N-1	1.2	2.6	2.9
	Ken 55-35	N-4	1.0	2.4	3.0

a) Experiments in the same item were conducted under same environmental conditions. b) Sub-division was not decided.

Table 2. Blast resistance of three varieties to Ken 53-33 estimated in termes of D values under different nitrogenous levels

Item of Exp.	N-level	Vars	Leaf order a)		
			1 st	2 nd	3 rd
B	High	Sensho	0.9	1.1	1.0
		Ginga	6.2	1.6	1.1
		Kamenoo	6.2	6.7	4.7
	Low	Sensho	1.0	0.9	0.9
		Ginga	4.1	1.4	1.1
		Kamenoo	5.2	7.8	6.3

a) counted from the top out of extruding leaf

Comparison of Ginga with Sensho and Kamenoo in genic system of resistance to Ken 53-33

According to combination between isolates and crosses, the results of Exp. C were divided into 4 sub-units, a, b, c, and d, and the former two were obtained by using Ken 53-33 as shown in Table 3. The results of inoculation were grouped in 3 tables; that is, segregation of resistance and laziness in F_2 plants in Table 3, the segregation in F_3 plants in Table 4 and resistance reaction of parental vars and F_1 in Table 5.

Lazy-Kamenoo was assumed to be similar in genic system to H-79 previously reported[3], and genotypes within a broad line in Figure A were used for susceptible F_2 plants of Exp. C-a according to the ratio of R:S=49:15. The recombination value of *Rb*$_1$-*la* was estimated at 5.0 %. As H. D. values of pedigrees of Exp. C-b and Exp. E were distributed within their parental vars, two genes, tentatively named as Rb'_2 and Rb'_3, were presumed to control the resistance of Ginga, and these are multiple alleles of Rb_2 and Rb_3 of Sensho or closely linked with them.

Lazy-Ginga × Sensho of Exp. C-b was about 5 % less than lazy-Kamenoo × Sensho of Exp. C-a in the number of susceptible F_2 plants. Two genotypes were reduced from 8 susceptible ones of Exp. C-a as illustrated in Figure B. The present assumption of genotype gave 7.0 % as the recombination value of *Rb*$_1$-*la*. Raised more susceptibly, materials of Exp. D-1 were about 4 % more than those of Exp. C-b in the number of susceptible F_2 plants as shown in Table 3. One genotype was added to Exp. C-b as a susceptible one as shown in the broken line in Figure B. These 7 genotypes were expected to be susceptible to both Ken 53-33 and Hoku 1 on the basis of the index-values assumed in Sensho × H-79[3]. Exp. D-1 gave 5.1 % as the recombination value of *Rb*$_1$-*la*.

Table 3. Segregation of blast resistance and laziness among F_2 plants of material crosses

Isolate	Item of Exp.	Cross		F_2 phenotype				Total
				R.normal	R.lazy	S.normal	S.lazy	
Ken 53-33	C-a	Sensho × lazy-Kamenoo	No. obs.	216	22	14	58	310
			Culc. 5.0%	217.1	20.2	15.4	57.3	310.0[a]
	C-b	Sensho × lazy-Ginga	No. obs.	197	24	7	39	267
			Culc. 7.0%	197.4	27.1	6.2	39.6	267.0[b]
	D-1	Sensho × lazy-Ginga	No. obs.	340	35	28	76	479
			Culc. 5.1%	363.8	44.9	22.4	74.9	479.0[c]
	E	Sensho × Ginga	No. obs.	157		61		218
	G	Ginga × Kamenoo	No. obs.	134		26		160
			Culc.	130.0		30.0		160.0[d]
Hoku 2	C-c	Sensho × lazy-Kamenoo	No. obs.	229	65	1	15	310
			Culc. 5.5%	230.9	65.3	0.8	13.8	310.0[e]
	F	Ginga × H-79	No. obs.	231	82	62	18	393
			Culc.	239.5	79.8	55.3	18.4	393.0[f]
	C-d	Ginga × Kamenoo	No. obs.	69		11		80
			Culc.	65.0		15.0		80.0[g]

a) R:S=49:15 $\chi^2=0.3019$ df=3 P=0.98-0.95 b) R:S=53:11 $\chi^2=0.5102$ df=3 P=0.95-0.90
c) R:S=51:13 $\chi^2=3.6292$ df=3 P=0.5-0.3 d) R:S=13:3 $\chi^2=0.6465$ df=1 P=0.5-0.3
e) R;S=61:3 $\chi^2=0.3747$ df=3 P=0.95-0.90 f) R:S=13:3 $\chi^2=1.1829$ df=3 P=0.90-0.80
g) R:S=13:3 $\chi^2=1.3129$ df=1 P=0.3-0.2

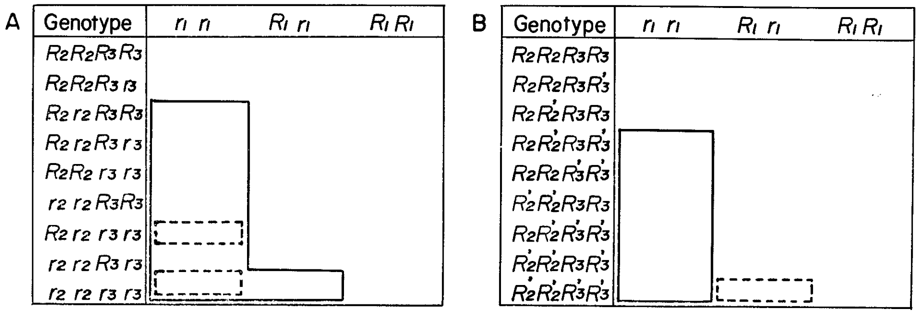

Fig. A and B Genotypes of the blast resistance of Sensho × lazy-Kamenoo and of Sensho × lazy-Ginga : *R*, *R′* and r′ stands for *Rb*, *Rb′* and *rb*, respectively. Eight genotypes of Fig. A surrounded with a broad line and two ones with a broken line are expected to be susceptible in Exp. C-a and Exp. C-c, expectively. Six genotypes of Fig. B surrounded with a broad line are expected to be susceptible in Exp. C-b and more one of a broken line is added in Exp. D-1.

Table 4. Segregation of blast resistance to Ken 53-33 of F_3 lines selected from Exp. D-1 of Table 3 and linkage relationship between laziness and Rb_1

Item of Exp.	Cross		F_3 phenotype				Total
			R.normal	R.lazy	S.normal	S. lazy	
D-2	Sensho × lazy-Kamenoo	No. obs.	48	5	147	63	263
		Culc. 31%	59.4	6.3	137.9	59.4	263.0[a]

a) R:S=1:3 χ^2=3.2743 df=3 P=0.50-0.30

Table 5. Blast resistance of parental vars and F_1 plants in each experiment

Isolate	Item of Exp.	Variety and F_1	Average of H. D.	Range of H. D.	Isolate	Item of. Exp	Variety and F_1	Average of H. D.	Range of H. D.
Ken 53-33	C-a -b	Sensho	1.2	1- 2	Ken 53-33	E	Sensho	1.9	1-3
		lazy-Ginga	7.1	4-12			Ginga	17.9	12-S
		lazy-Kamenoo	11.9	4-S[a]		G	Ginga	1.9	1- 3
		F_1[b]	1.4	1- 2			Kamenoo	8.5	3-12
	D-1	Sensho	1.5	1- 2	Hoku 2	C-c -d	Sensho	1.0	1
		lazy-Ginga	7.4	4-12			lazy-Ginga	1.1	1-2
		Kamenoo	12.5	8- S			lazy-Kamenoo	5.0	4-8
		F_1[c]	1.3	1- 2			F_1[b]	1.0	1
	D-2	Sensho	1.4	1- 2		F	Ginga	1.4	1-2
		lazy-Ginga	8.3	4-12			H-79	9.2	3-S
		Kamenoo	10.6	6- S			F_1	1.8	1-2
		F_1[c]							

a) S means more susceptible plants than others and is evaluated as 20 in H. D.
b) F_1 of Sensho × lazy-Kamenoo c) F_1 of Sensho × lazy-Ginga

Two of 20 F_3 lines revealed that they were homogenously normal in laziness, and 14 of 15 lines gave segregants in resistance to Ken 53-33. Data of 12 lines segregated in both the characters were totalized in Table 4. In the present experiment, Rb_1 behaved as a recessive genes and its recombination value between *la* was computed at 31 % far more different from the others.

Sensho × Ginga in Exp. E presented a large number of susceptible F_2 plants in Table 3 than Sensho × lazy-Ginga in Exp. C and Exp. D under more susceptible conditions as shown by parental vars of Table 5. Exp. E indicated the presence of susceptible genotypes more than illustrated in Figure B, but no further analysis was followed because *la* was not available in the present cross.

These two genes of Ginga presented a good fit to digenic segregation of R:S= 13 : 3 in F_2 plants in Exp. G, in which materials were more resistant to Ken 53-33 than in other experiments as shown in Table 5. But under ordinary raising conditions as conducted in Exp. C, Kamenoo could not give data of Ken 53-33 valid to genic analysis of Ginga in blast resistance because the parental 2 vars overlaped in the range of H. D. values and the distribution of F_2 plants were not available to discriminate clearly between 2 groups, R and S. On the contrary, Hoku 2 was useful for the present pourpose because of its mild virulency.

Comparison of Ginga with Sensho and Kamenoo in the genic system of resistance to Hoku 2

In Exp. F, all of the 90 plants showed the same response to both Hoku 2 and Ken 54-04. Sensho of Exp. C-c presented less susceptible F_2 plants than Ginga of Exp. C-d, and all of them were susceptible to Ken 53-33 with which they were inoculated in Exp. C-a. Two genotypes surrounded with a broken line as shown in Figure A were assumed to be susceptible to Hoku 2 and the recombination value of Rb_1-la was computed at 5 %.

As there was no segregant more susceptible than lazy-Ginga in pedigree of Sensho × Ginga of Exp. C and Exp. D-2, the relationship of $Rb'_2 \cdot Rb'_3$—$Rb_2 \cdot Rb_3$ in resistance to Hoku 2 was ascertained too. Further, Ken 54-04 caused no segregant to 137 F_2 plants of Sensho × Ginga (unpublished). Ginga gave a good fit to a R:S =13:3 ratio of F_2 plants in Exp. C-d and Exp. F, and in the latter subject revealed the independency of its resistance genes from *la*. Thirteen F_3 lines raised from susceptible F_2 plants of Fxp. F were observed in their segregation of resistance as follows ; 3 lines were homogenously susceptible, 5 segregated a small number of pedigrees as resistant as Ginga and the other 5 more resistant than H-79. Thus, Rb_1 was responsible for a significant part of the difference between Ginga and Sensho in resistance to Hoku 2 as well as to Ken 53-33. Hoku 2 was available to detect a digenic behaviour of Ginga under raising conditions of Exp. C and Exp. F.

Linkage relationships between resistance genes of Ginga and marker genes other than la

Material crosses of 6 testers gave a good fit to monogenic F_2 segregation of each marker gene tested, and to digenic segregation of resistance to Hoku 2. All of the tested genes were independent of the resistance genes of Ginga, as shown in Table 6. These marker genes were also as independent as the genes of Sensho (unpublished).

Table 6. Test of independence between blast resistance genes of Ginga and genes of other characters

Item of Exp.	Stock No.[b)]	Marker gene	Segregation ratio of		Combined character in F_2 plants					Goodness of fit	
			R:S	M:m	RM	Rm	SM	Sm	Total	χ^2	P
	H-69	*fs_1*	13:3	3:1	95	27	18	9	149	1.5334	0.7-0.5
	H-69	*nl*	13:3	3:1	91	31	20	7	149	0.0692	-0.99
	H-90	*gl*	15:1	3:1	115	30	11	3	159	3.3717	0.5-0.3
	A- 5	*Rc*	12:4	1:3	37	93	6	28	154	3.7979	0.3-0.2
H[a)]	H-75	*Rc*	12:4	1:3	32	92	7	25	156	1.8725	0.7-0.5
	H-75	*gh*	12:4	3:1	94	30	25	7	156	1.8638	0.7-0.5
	N-53	*Dn*	12:4	1:3	18	58	2	17	95	2.9947	0.5-0.3
	H-79	*lg*	13:3	3:1	141	49	38	12	240[c)]	0.7859	0.9-0.8
	H-79	*bc*	13:3	3:1	239	74	64	16	393[c)]	2.1043	0.7-0.5

a) Those genic analysis were conducted under environmental conditions different from each other. b) Stock number of Plant Breeding Institute, Faculty of Agriculture, Hokkaido University c) The same materials of Exp. F of Table 3 were used.

Discussion

The moderate level of the blast resistance of Ginga to Hoku 1 observed in the present study had already been ascertained with the same three vars as was used in Exp. B, and the sheath test revealed its validity to indicate the degree of blast resistance precisely[14,15]. Ginga always showed such a level in reaction to a wide racial range of Japanese isolates which were grouped into 47 patterns[16] differentiated by Sensho, Ginga and Norin 20 together with other 35 vars, that is, any of them could not cause more susceptible reactions to Sensho than to Ginga. On the other hand Norin 20 was always more susceptible than Ginga, giving S-reaction in all patterns[16].

Tasensho was on the level similar to Shinju, Futaba and Ginga in resistance to the two isolates[10]. Shinju and Futaba were reported by Iwatsuki[8], the chief researcher of the breeding program started from Sensho, to be far more highly resistant than other Japanese domestic lowland vars, but remained slightly more susceptible than their parent, Sensho. Sensho, Shuho, Ginga and Kamenoo were scored as 1.1, 2.7, 2.8 and 4.9, respectively, in the averge of resistance to 9 isolates[4], that is, Shuho was almost the same as Ginga in resistance level. The similar D values estimated by the writer (unpublished), suggested that Shuhu, Futaba, Ginga and Homare-Nishiki were more susceptible in resistance to Ken 53-33 and to Hoku 1 than Sensho. From these observations, the decline of blast resistance was assumed to have commenced in the early stage of the program, — in the stage of Shinju and Futaba, or probably earlier in the stage of Tasensho.

The above-mentioned decline of resistance was reasonably understood from the behaviour of Rh_1 traced immediately by genic analysis of Sensho × lazy-Ginga, and this assumption was supported by the comparison among genic analysis of 3 crosses, Sensho × lazy-Kamenoo, Ginga × H-79 and Sensho × H-79 previously reported[3]. The similar decline was observed in Homare-Nishiki with the materials from cross of H-79 (unpublished).

These analysis revealed that the descendants of Sensho had failed to incorporate Rb_1 with the result that the high blast resistance of the parent declined. The same consequences were observed in the case of Zenith and 54BC-68, which is the intermediate parent of cultivars of *Pi-z*. That is, Rb_6 of Zenith linked with *la* was not transferred to the latter line[5] and its following vars[6], and these derivatives were more or less inferior to Zenith in blast resistance[2,6].

Rb_1 behaved as a recessive gene in F_3 lines of the back-ground of Ginga as illustrated in Figure B, and so the present gene was expected to behave as follows ; it varies in dominancy with its cooperate gene (s) substituted by Japanese lowland vars and makes it difficult to select progenies with the same resistance as Sensho. As to the recombination value of Rb_1-*la* the result of Exp. D-2 of F_3 lines was inconsistent with those of the other experiments and suggested the presence of other gene(s) in addition to Rb'_2 and Rb'_3. These two problems raised by the test of F_3 lines seemed to be very important to breeding procedures as well as to genic analysis.

Though keeping its higher blast resistance to Japanese isolates than Ginga, Sensho was expected to show race specific reaction owing to its olygogenic system of Rb_1 and it was actually indicated by spray inoculation of USA races, that is, 2 of 10 races gave reverse order between Sensho and Ginga in pathogenic reaction[1]. However, liable to vary with many inoculation factors, the moderate resistance of Ginga was controlled by the two genes in the present study and by the 3 genes, one major and 2 minor ones, in the previous report[11]. The genic system consisting of a small number of genes caused to a few foreign isolates an order reverse to that indicated by Japanese and many other isolates and two vars, Ginga and Norin 20 [1,15]. Thus, the oligogenic systems with race specific effects were responsible for the blast resistance of Sensho and of Ginga. The present results inconsisted with the assumption that Sensho and Ginga have their own level of "field resistance" expected to be controlled by polygenic systems with non-specific effects as reviewed in some reports[2].

With regard to the marker genes tested, there was no linkage relation available for the genic analysis of Ginga as well as of Sensho other than Rb_1-*la* relation.

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和 文 摘 要

いもち病抵抗性の遺伝

Ⅲ戦捷の子孫品種銀河におけるいもち病抵抗性の低下

後藤　岩三郎

標識品種 H-79 に銀河をもどし交配し，その B_5F_4 からもつれ銀河を育成した。もつれ（*la*）は戦捷の Rb_1 と密接に連鎖する。戦捷×もつれ銀河，戦捷×もつれ亀の尾，銀河×H-79 等の分析から次のことが明らかになった。（1）銀河には戦捷の Rb_1 がとりこまれていない。これが銀河のいもち病抵抗性を低下させる主な要因と考えられる。田戦捷，真珠，双葉，秀峰やほまれ錦も銀河と同程度の抵抗性を示し，戦捷よりは弱い。したがって戦捷の高度抵抗性導入の育種過程の早い段階で低下したものである。（2）銀河には2対の抵抗性遺伝子があり，その相加的な効果で本品種の中程度の抵抗性を支配する。この2対は戦捷の他の2対の抵抗性遺伝子と複対立関係にあるか，あるいは極めて近く連鎖する。