Studies on Genetics and Breeding of Resistance to Bacterial Leaf
Blight in Rice. VI. Inheritance of Quantitative Resistance
of the Variety IR 28 to Bacterial Groups II, III and IV of
Xanthomonas campestris pv. *oryzae* of Japan¹⁾

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Inheritance of quantitative resistance of IR 28 was studied through the analysis of 6 populations, P₁, P₂, F₁, F₂, B₁ and B₂, derived from each of two crosses, Toyonishiki/IR 28 and Todorokiwase/IR 28. In both the crosses, F₂, B₁ and B₂ populations showed each a continuous variation in the resistance to each bacterial group. In some combinations of plant material and bacterial group, it was proved that transforming the original data into square roots was the most adequate for the analysis by additive-dominance model, and the major contribution to population mean was made by additive gene effects. There were some other cases where data were not fit for additive-dominance model through every kind of transformation attempted. In these cases, the effect of a digenic interaction remained yet in the total effect of all the genes controlling the resistance, though additive gene effects were also significant. Both heritabilities in a narrow sense and in a broad sense proved to be significantly different from zero and fairly high, suggesting that the selection for the resistance at an early generation of hybrid is effective. Quantitative resistances to bacterial groups II, III and IV highly correlated with each other both genetically and phenotypically. These high correlations probably make it possible to select the plants non-specifically resistant to all the three bacterial groups by the inoculation of only one of them.

KEY WORDS : *Oryza*, *Xanthomonas*, disease resistance, genetics, heritability, genetic correlation.

Introduction

In bacterial leaf blight of rice caused by *Xanthomonas campestris* pv. *oryzae* (Ishiyama 1922) Dye 1978, there are two types of resistance which differ in their specificity to the race of the pathogen. One is the qualitative resistance which is specific to the race, and the other is the quantitative resistance which does not appear to show any specificity to the race. The latter is essentially important for a breeding program, but its genetic study has not sufficiently been made as yet.

IR 28 has qualitative resistances to bacterial groups I and V, and also has quantitative resistances to bacterial groups II, III and IV (HORINO and YAMADA 1979). On the inheritance of quantitative resistance of IR 28 to these three bacterial groups, YAMADA *et al.* (1979) presented a few results, which showed that the heritabilities in a broad sense of those resistances were high, and there were high positive genotypic correlations between those resistances. In that report, however, environmental variances and covariances were estimated only from genetically uniform populations. Therefore, it is yet apprehended that they have not always represented the true environmental components in the F₂ generation, and besides the heritabilities and genotypic correlations were biased by the strong effects of genetically unfixable variation, if any.

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In the present study, not only F_2 populations but also first backcross populations were used as the segregating generation to remove the above apprehension.

Materials and Methods

1. Plant material

IR 28 was crossed with two Japanese varieties, Toyonishiki and Todorokiwase, both of which possess a low degree of quantitative resistance. The F_1 hybrids were self-pollinated to produce F_2 populations, and were backcrossed with each parent to produce first backcross populations, B_1 and B_2 , which represented the backcrosses with either of the Japanese varieties and with IR 28, respectively. Cross combinations of Toyonishiki/IR 28 and Todorokiwase/IR 28 are hereafter referred to as Cross 1 and Cross 2, respectively. For each of the cross combinations, six populations, P_1 , P_2 , F_1 , F_2 , B_1 and B_2 , were thus prepared and grown in an experimental paddy field with randomized block design. Parents and F_1 's were assigned each two plots for the experiment, while each of F_2 's and each of backcross populations were assigned eight and six plots, respectively. Forty-six plants were grown in a plot, except for the plots of the B_1 from Cross 1, which contained 30 plants each.

2. Inoculation

T 7147 of the group II, T 7133 of the group III and H 75373 of the group IV were used as the bacterial strains standing for the respective groups. These strains were cultured on the potato semisynthetic agar medium at 28°C for two days, then suspended in distilled water at a concentration of 10^7 – 10^8 cells/ml. Each strain was checked for the pathogenicity typical of the bacterial group to which it belongs, then used for inoculation. The inoculation was applied to the central parts of fully-developed leaves of mature plants by double needle-prick method. Two leaves per plant were assigned to each bacterial strain. Six leaves per plant were consequently subjected to the inoculation with three bacterial strains.

For convenience of description, a combination of plant material and bacterial group will frequently be expressed by the abbreviation with the symbol /. For instance, "Cross 1/II" means that the plant materials from Cross 1 were inoculated with the strain of bacterial group II.

3. Measurement of disease-severity and statistical analysis

Three weeks later, disease-severity of inoculated plants was expressed by the disease-index (from 0=most resistant, to 7=most susceptible) according to the standard proposed by EZUKA and HORINO (1974). Degree of resistance of a plant to every bacterial group was evaluated on the basis of the mean value of disease-indices on two leaves inoculated.

To detect a scale adequate for additive-dominance model, individual scaling tests proposed by MATHER (1949) were used. Heritability in a narrow sense (h_N^2) was estimated by the method of WARNER (1952), $[2V_{F_2} - (V_{B_1} + V_{B_2})]/V_{F_2}$, and heritability in a broad sense (h_B^2) was estimated by the method of WEBER and MOORTHY (1952), $[V_{F_2} - 1/3(V_{P_1} + V_{P_2} + V_{F_1})]/V_{F_2}$. Phenotypic (r_{PH}), genotypic ($r_{G(B)}$) and genetic ($r_{G(N)}$) correlation coefficients between the quantitative resistances to the three bacterial groups were also estimated by next formulae:

$$r_{PH} = \frac{\text{Cov}_{F_2AB}}{\sqrt{V_{F_2A} \cdot V_{F_2B}}} \quad (\text{WEBER and MOORTHY 1952})$$

$$r_{G(B)} = \frac{\text{Cov}_{F_2AB} - \text{Cov}_{EAB}}{\sqrt{(V_{F_2A} - V_{EA})(V_{F_2B} - V_{EB})}} \quad (\text{WEBER and MOORTHY 1952})$$

$$r_{G(N)} = \frac{2 \text{Cov}_{F_2AB} - (\text{Cov}_{B_1AB} + \text{Cov}_{B_2AB})}{\sqrt{[2V_{F_2A} - (V_{B_1A} + V_{B_2A})][2V_{F_2B} - (V_{B_1B} + V_{B_2B})]}} \quad (\text{UKAI 1974})$$

where V_{F_2A} , V_{B_1A} and V_{B_2A} are the phenotypic variances observed in the character A of F_2 , B_1 and B_2 populations, respectively. V_{F_2B} , V_{B_1B} and V_{B_2B} are the phenotypic variances observed in the character B of F_2 , B_1 and B_2 populations, respectively. V_{EA} and V_{EB} are the environmental variances in the characters A and B, respectively and were calculated by averaging the three variances of parents and F_1 populations. Cov_{F_2AB} , Cov_{B_1AB} and Cov_{B_2AB} are the phenotypic covariances between the characters A and B of F_2 , B_1 and B_2 populations, respectively. Cov_{EAB} is the environmental covariance between the characters A and B, and was calculated by averaging the three covariances of parents and F_1 populations.

A part of the calculation was made with the computer system at the Research Computer Center of the Ministry of Agriculture, Forestry and Fisheries.

Results

1. Frequency distribution

F_2 , B_1 and B_2 populations derived from Crosses 1 and 2 showed each a continuous variation in the resistance to each bacterial group as exemplified in Fig.1. Mendelian method could not be applied to genetic analysis of the variation because the grouping of plants by resistance degree was actually impossible.

2. Detection of adequate scale and analysis of population mean

To find out a scale adequate for the analysis by additive-dominance model, individual scaling tests were first conducted on the original, square root (square roots of the original data) and logarithmic (common logarithms of the original data plus 1.0) scales.

As regards original scale, individual scaling tests revealed at least a significant departure from zero in every combination of plant material and bacterial group except for Cross 2/IV (Tables 1 and 2). This clearly indicates that original scale is inadequate for the analysis by additive-dominance model.

As regards square root scale, on the other hand, individual scaling tests yielded some significant departures in Cross 1/II, Cross 2/II and Cross 2/III, but did not any in Cross 1/III, Cross

Fig.1. Frequency distributions of plants showing various degrees of resistance to bacterial group III (T 7133)

Table 1. Means of degrees of resistance and their standard errors, and scaling tests with original scale for the six populations from the cross between Toyonishiki and IR 28 (Cross 1)

Item	Bacterial group ¹⁾		
	II	III	IV
Population			
P ₁	3.55±0.062	4.80±0.078	4.79±0.075
P ₂	2.34±0.044	2.68±0.059	2.07±0.042
F ₁	3.07±0.058	3.88±0.084	2.85±0.057
F ₂	3.00±0.065	3.94±0.080	3.22±0.076
B ₁	3.38±0.072	4.32±0.098	3.67±0.101
B ₂	2.99±0.049	3.43±0.058	2.40±0.040
Scaling tests ²⁾			
A	0.14±0.167	-0.04±0.226	-0.30±0.222
B	0.57±0.121**	0.31±0.155*	-0.13±0.106
C	-0.04±0.293	0.54±0.374	0.31±0.334
D	-0.37±0.156*	0.13±0.196	0.37±0.186*

1) : T7147, T7133 and H75373 were used as bacterial strains of groups II, III and IV, respectively.

2) : $A=2\bar{B}_1-\bar{P}_1-\bar{F}_1$, $V_A=4V_{\bar{B}_1}+V_{\bar{P}_1}+V_{\bar{F}_1}$.
 $B=2\bar{B}_2-\bar{P}_2-\bar{F}_1$, $V_B=4V_{\bar{B}_2}+V_{\bar{P}_2}+V_{\bar{F}_1}$.
 $C=4\bar{F}_2-2\bar{F}_1-\bar{P}_1-\bar{P}_2$, $V_C=16V_{\bar{F}_2}+4V_{\bar{F}_1}+V_{\bar{P}_1}+V_{\bar{P}_2}$.
 $D=2\bar{F}_2-\bar{B}_1-\bar{B}_2$, $V_D=4V_{\bar{F}_2}+V_{\bar{B}_1}+V_{\bar{B}_2}$.

*, **: Significant at 0.05 and 0.01 levels of probability, respectively.

Table 2. Means of degrees of resistance and their standard errors, and scaling tests with original scale for the six populations from the cross between Todorokiwase and IR 28 (Cross 2)

Item	Bacterial group ¹⁾		
	II	III	IV
Population			
P ₁	3.73±0.073	5.58±0.089	5.55±0.063
P ₂	2.34±0.044	2.68±0.059	2.07±0.042
F ₁	3.40±0.069	4.23±0.101	3.01±0.065
F ₂	3.38±0.065	4.55±0.080	3.52±0.079
B ₁	3.99±0.077	5.23±0.086	4.34±0.099
B ₂	3.13±0.050	3.48±0.058	2.52±0.041
Scaling tests ²⁾			
A	0.86±0.184**	0.66±0.219**	0.12±0.217
B	0.51±0.129**	0.05±0.164	-0.03±0.113
C	0.65±0.305*	1.49±0.394**	0.46±0.351
D	-0.36±0.158*	0.39±0.191*	0.18±0.191

1), 2), * and **: See notes of Table 1.

1/IV and Cross 2/IV (Tables 3 and 4). For the latter cases, therefore, square root scale was considered to be good for additive-dominance model. Based on this inference, three components (MATHER 1949), m , $[d]$ and $[h]$, of additive-dominance model in square root scale were estimated by weighted least squares technique (Table 5). Table 5 indicates

Table 3. Means of degrees of resistance and their standard errors, and scaling tests with square root scale for the six populations from the cross between Toyonishiki and IR 28 (Cross 1)

Item	Bacterial group ¹⁾		
	II	III	IV
Population			
P ₁	1.878±0.0155	2.185±0.0172	2.181±0.0177
P ₂	1.523±0.0141	1.629±0.0183	1.430±0.0150
F ₁	1.742±0.0156	1.959±0.0209	1.681±0.0163
F ₂	1.696±0.0182	1.947±0.0204	1.753±0.0199
B ₁	1.819±0.0196	2.053±0.0238	1.883±0.0258
B ₂	1.712±0.0141	1.834±0.0162	1.533±0.0127
Scaling tests ²⁾			
A	0.017±0.0449	-0.037±0.0547	-0.096±0.0570
B	0.159±0.0352**	0.080±0.0426	-0.045±0.0337
C	-0.103±0.0820	0.058±0.0950	0.038±0.0891
D	-0.140±0.0437**	0.007±0.0499	0.089±0.0491

1), 2) and **: See notes of Table 1.

Table 4. Means of degrees of resistance and their standard errors, and scaling tests with square root scale for the six populations from the cross between Todorokiwase and IR 28 (Cross 2)

Item	Bacterial group ¹⁾		
	II	III	IV
Population			
P ₁	1.923±0.0179	2.355±0.0187	2.353±0.0133
P ₂	1.523±0.0141	1.629±0.0183	1.430±0.0150
F ₁	1.835±0.0185	2.045±0.0240	1.727±0.0181
F ₂	1.808±0.0173	2.101±0.0196	1.833±0.0205
B ₁	1.973±0.0191	2.264±0.0200	2.044±0.0240
B ₂	1.752±0.0141	1.847±0.0153	1.574±0.0129
Scaling tests ²⁾			
A	0.188±0.0460**	0.128±0.0502*	0.009±0.0530
B	0.146±0.0365**	0.021±0.0429	-0.008±0.0349
C	0.116±0.0816	0.331±0.0955**	0.097±0.0919
D	-0.109±0.0419*	0.091±0.0466	0.048±0.0492

1), 2), * and **: See notes of Table 1.

that additive gene effect makes highly significant contribution to each population mean of Cross 1/III, Cross 1/IV and Cross 2/IV, and dominance gene effect is relatively less important than additive one. The sign of dominance gene effect was positive in Cross 1/III but negative in Cross 1/IV and Cross 2/IV.

Also as regards logarithmic scale, additive-dominance model was not applicable in Cross 1/II, Cross 2/II and Cross 2/III as in square root scale (Table 6). Hence for these combinations, a model involving digenic interactions was applied to the data with square root scale, and the perfect fit estimates of three interaction components, [i], [j] and [l], were calculated in addition to m, [d] and [h] by the formulae of JINKS and JONES (1958), as shown in Table 7. In Cross 1/II, all the six estimates including [i], [j] and

Table 5. Weighted least squares estimates and their standard errors of the additive and dominance components of means in square root scale for resistance

Component	Cross combination/ Bacterial group ¹⁾	P
Cross 1/III		
m	1.913±0.0116	<0.001
[d]	0.267±0.0114	<0.001
[h]	0.060±0.0229	0.010~0.005
Cross 1/IV		
m	1.799±0.0107	<0.001
[d]	0.376±0.0106	<0.001
[h]	-0.131±0.0194	<0.001
Cross 2/IV		
m	1.892±0.0093	<0.001
[d]	0.463±0.0092	<0.001
[h]	-0.162±0.0192	<0.001

1) Cross 1 : Toyonishiki/IR 28.

Cross 2 : Todorokiwase/IR 28.

III : T7133 was used as bacterial strain of the group III.

IV : H75373 was used as bacterial strain of the group IV.

sible in additive-dominance model, may be partly attributed to that somewhat larger sampling error was introduced into the values of h_N^2 . In Cross 2/II and Cross 2/IV, the values of h_B^2 were higher than those of h_N^2 . This may suggest the presence of dominance effect.

4. Correlation coefficient

Phenotypic, genotypic and genetic correlation coefficients between the quantitative resistances to bacterial groups II, III and IV are summarized in Table 9. Phenotypic correlation coefficients were all positive and significantly different from zero. Genotypic and genetic correlation coefficients were also positive and fairly high, though the former and the latter ranged from 0.668 to 0.853 and 0.507 to 0.823, respectively.

[1] were significant. In Cross 2/II, five estimates including [i] and [l] were significant. In Cross 2/III, all the three interaction components were not significant as dominance effect, but additive-dominance model was not applicable as previously pointed. These results suggest that some other more complicated factor(s) may contribute an effect to the population mean.

3. Heritability

Both heritabilities in a narrow sense and in a broad sense which were estimated with square root scale are summarized in Table 8. As this table shows, they were all significantly different from zero and fairly high. In each of Cross 1/II, Cross 1/III, Cross 1/IV and Cross 2/III, the values of h_B^2 were all slightly lower than those of h_N^2 . Such a phenomenon, which should be impos-

Table 6. Scaling tests with logarithmic scale for resistance

Scaling tests ²⁾	Cross combination/Bacterial group ¹⁾		
	Cross 1/II	Cross 2/II	Cross 2/III
A	0.002±0.0164	0.060±0.0161**	0.037±0.0166*
B	0.059±0.0133**	0.054±0.0136**	0.009±0.0154
C	-0.055±0.0305	0.031±0.0297	0.107±0.0328**
D	-0.058±0.0163**	-0.042±0.0152**	0.030±0.0160

1) Cross 1 : Toyonishiki/IR 28.

Cross 2 : Todorokiwase/IR 28.

II : T7147 was used as bacterial strain of the group II.

III : T7133 was used as bacterial strain of the group III.

2), * and **: See notes of Table 1.

Table 7. Perfect fit estimates and their standard errors of the additive, dominance and digenic interaction components of means in square root scale for resistance

Component	Cross combination/ Bacterial group ¹⁾	P
Cross 1/II		
m	1.422±0.0881	<0.001
[d]	0.177±0.0105	<0.001
[h]	0.776±0.2086	<0.001
[i]	0.279±0.0875	0.005~0.001
[j]	-0.142±0.0527	0.010~0.005
[l]	-0.455±0.1268	<0.001
Cross 2/II		
m	1.506±0.0846	<0.001
[d]	0.200±0.0114	<0.001
[h]	0.880±0.2021	<0.001
[i]	0.218±0.0838	0.010~0.005
[j]	0.043±0.0526	0.500~0.400
[l]	-0.551±0.1251	<0.001
Cross 2/III		
m	2.174±0.0940	<0.001
[d]	0.363±0.0131	<0.001
[h]	-0.163±0.2223	0.500~0.400
[i]	-0.182±0.0931	0.100~0.050
[j]	0.107±0.0567	0.100~0.050
[l]	0.033±0.1387	>0.500

1) : See notes of Table 6.

Table 8. Heritabilities of resistance in the F₂ generation

Cross combination	Item	Bacterial group ¹⁾		
		II	III	IV
Toyonishiki/ IR 28	h_B^2	0.829**	0.786**	0.831**
	h_N^2	0.985**	0.862**	0.872**
Todorokiwase/ IR 28	h_B^2	0.760**	0.727**	0.855**
	h_N^2	0.586**	0.765**	0.676**

1) and **: See notes of Table 1.

Table 9. Phenotypic, genotypic and genetic correlations in the F₂ generation between resistances to bacterial groups II, III and IV

Bacterial group ¹⁾	Item	Bacterial group ¹⁾		
		II	III	IV
II	Phenotypic ²⁾		0.681**	0.624**
	Genotypic ³⁾		0.833	0.751
	Genetic ⁴⁾		0.814	0.685
III	Phenotypic	0.659**		0.579**
	Genotypic	0.853		0.668
	Genetic	0.823		0.544
IV	Phenotypic	0.561**	0.617**	
	Genotypic	0.673	0.796	
	Genetic	0.507	0.665	

Right side of diagonal : Toyonishiki/IR 23.

Left side of diagonal : Todorokiwase/IR 23.

1) and **: See notes of Table 1.

2) : Phenotypic correlation.

3) : Genotypic correlation.

4) : Genetic correlation.

Genotypic and genetic correlations were not checked for significance.

Discussion

Some reports (ANDO *et al.* 1973, YAMAMOTO *et al.* 1977) indicated that the quantitative resistance to bacterial leaf blight in rice had horizontal nature, that is, did not show any specificity to the race of pathogen. This horizontal nature of resistance is essentially important for a breeding program, because it will refuse the breakdown caused by the shift of pathogen races. A disease resistance having the horizontal nature is, however, not a little difficult to treat in a breeding program, because it in most cases gives rise to continuous variations in segregating generations and thus makes the identification of the gene or genes responsible for it almost impossible. The quantitative resistance investigated in the present study also showed a continuous variation without any distinct classes in every segregating generation. Therefore instead of Mendelian approach, the method of biometrical genetics must have been taken up for the analysis of the inheritance to get useful information for actual selection.

There are instances where several factors cause a bias against an estimate of a genetic parameter as MATHER (1949) pointed out. These factors are the presences of 1) multiple alleles, 2) linkages, 3) lethal genes, 4) unequal viability among genotypes, 5) significant genotype $\times$ environment interaction and/or 6) significant epistatic effects. In the present study, there would be no room for the first factor to act, because the parental varieties used in the present study were homozygous. Furthermore, no serious bias from factors 3 and 4 would be expected either.

The effect of linkage could not be investigated in the present study, since only F_2 and first backcross populations were used as the segregating generation. With the effect of genotype $\times$ environment interaction, it may be difficult without further experiments at many locations and in many years to conclude whether it can be ignored or not. However, the magnitude of bias caused by it must have been minimized, since all the materials were studied under an artificial epiphytotic condition.

As regards the last factor, MATHER (1949) pointed out that even if there were modifications of phenotypic variation due to non-allelic interaction, an adequate scale could remove the effect of interaction and enabled the analysis by additive-dominance model. With respect to this, scaling tests clearly proved that square root scale was adequate for additive-dominance model so far as Cross 1/III, Cross 1/IV and Cross 2/IV were concerned, and the analysis of the population means by this scale revealed that on the manifestation of resistance, additive effect was more important than dominance one. The disease-index used in the present study is an area character. MATHER (1949) suggested the possibility that in the case of an area character, a square root scale gave the strongest validity to the analysis by additive-dominance model. The results obtained from Cross 1/III, Cross 1/IV and Cross 2/IV confirm his suggestion. For the other cases where square root scale was not fit to additive-dominance model, attention should be paid to that digenic interaction and/or some other more complicated factor(s) may have introduced some bias into the estimates of genetic parameters.

The result of the present experiment indicated that the heritabilities of quantitative resistance were fairly high in the F_2 generation. The level of those estimates is almost equal to that of heading date and culm length of rice plant which appeared in some papers (TORIYAMA and FUTSUHARA 1958, HORIE *et al.* 1964). In most projects of rice breeding, heading date and culm length have so far positively been selected at an early generation of hybrid, and their genetic gains by this type of selection have been proved to be large enough. Therefore, it can naturally be said that a positive selection at an early generation of hybrid is effective also for the quantitative resistance to bacterial leaf blight.

The result of this experiment indicated also that in the F_2 generation, the quantitative resistances to bacterial groups II, III and IV highly correlated with each other both genetically and phenotypically. These high correlations should make it feasible to select the plants non-specifically resistant to all the bacterial groups used in this experiment by means of the inoculation of only one of them.

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Literature Cited

- ANDO, T., T. YAMAMOTO and M. YAMADA 1973. The quantitative resistance of rice varieties to bacterial leaf blight. Proc. Assoc. Pl. Prot. Hokuriku **21** : 32~35 (in Japanese).
- EZUKA, A. and O. HORINO 1974. Classification of rice varieties and *Xanthomonas oryzae* strains on the basis of their differential interactions. Bull. Tokai-Kinki Natl. Agric. Exp. Stn. **27** : 1~19.
- HORIE, M., K. SAIO, M. HATAMURA and A. ITO 1964. The estimators of heritability on paddy rice plants, soybean plants and silkworms. II. Paddy rice plants. Japan. J. Breed. **14** : 130~140 (in Japanese with English summary).
- HORINO, O. and T. YAMADA 1979. Resistance of rice varieties bred at IRRI to five pathotypes of *Xanthomonas oryzae* (Uyeda et Ishiyama) Dowson existing in Japan. Proc. Assoc. Pl. Prot. Hokuriku **27** : 12~18 (in Japanese with English summary).
- JINKS, J. L. and R. M. JONES 1958. Estimation of the components of heterosis. Genetics **43** : 223-234.
- MATHER, K. 1949. Biometrical Genetics. Methuen, London.
- TORIYAMA, K. and Y. FUTSUHARA 1958. Estimates of heritabilities on individuals and lines in rice. Japan. J. Breed. **7** : 208~212 (in Japanese with English summary).
- UKAI, Y. 1974. Estimation of genetic parameters. Breeding Handbook (ed. by T. MATSUO). Yokendo, Tokyo. 349~381 (in Japanese).
- WARNER, J. N. 1952. A method for estimating heritability. Agron. J. **44** : 427~430.
- WEBER, C. R. and B. R. MOORTHY 1952. Heritable and nonheritable relationships and variability of oil content and agronomic characters in the F_2 generation of soybean crosses. Agron. J. **44** : 202~209.
- YAMADA, T., O. HORINO and S. SAMOTO 1979. Studies on genetics and breeding of resistance to bacterial leaf blight in rice. IV. Inheritance of resistance of IR 28 to bacterial groups I, II, III, IV and V of *Xanthomonas oryzae* (Uyeda et Ishiyama) Dowson from Japan. Japan. J. Breed. **29** : 279~286 (in Japanese with English summary).
- YAMAMOTO, T., HARTINI R. H., MUHAMMAD M., T. NISHIZAWA and D. M. TANTERA 1977. Variation in pathogenicity of *Xanthomonas oryzae* (Uyeda et Ishiyama) Dowson and resistance of rice varieties to the pathogen. Contr. Centr. Res. Inst. Agric. Bogor **28** : 1~22.

イネ白葉枯病抵抗性に関する遺伝・育種学的研究

Ⅵ. IR 28 の日本産白葉枯病菌Ⅱ, ⅢおよびⅣ群菌系に対する量的抵抗性の遺伝

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国際稲研究所 (IRRI) で育成された IR 28 は、日本産白葉枯病菌Ⅱ, ⅢおよびⅣ群菌系に対して強い量的抵抗性を示す品種である。IR 28 を共通の抵抗性親とする二つの交配組合せについて、それぞれ両親品種、 F_1 , F_2 , B_1 および B_2 の 6 集団を供試し、各集団とⅡ, Ⅲ, Ⅳ各群の菌系を組合せて量的抵抗性の遺伝解析を行った。

まず尺度検定を行い、相加・優性効果のモデルによる解析には平方根尺度が適当であることを認めた。そこでこの尺度を用いて量的抵抗性に関する平均値の構成要素を推定した結果、相加的遺伝子効果、優性効果ともに統計的に有意であるが、前者の方が著しく大きいことが明らかとなった。

一部に、相加・優性効果のモデルによる解析に適当な尺度を見出すことのできない組があったが、これらの場合には、相加的遺伝子効果および優性効果のほかにエピスタシス効果をも考慮する必要があることが推測された。

平方根尺度を用いてⅡ、ⅢおよびⅣ群菌系に対する量的抵抗性の遺伝力ならびに抵抗性相互間の相関関係を調べた結果、 F_2 世代における広義ならびに狭義の遺伝力はいずれも統計的に有意で高い値を示すこと、および抵抗性相互間の表現型相関、遺伝子型相関および遺伝相関はいずれも正の高い値を示すことが明らかとなった。これらの結果に基づき、IR 28 に由来するⅡ、ⅢおよびⅣ群菌系に対する量的抵抗性の選抜は雑種初期世代から有効であり、しかも選抜には全菌系を接種する必要はなく、いずれか一つの菌系の接種で十分に効果的な選抜が可能であると推論した。