Strain-Specific Reaction of Field Resistance of Japanese Rice
Varieties Revealed with Philippine Strains of Rice Blast
Fungus, *Pyricularia oryzae* Cav.

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Twenty four Japanese varieties with known level of field resistance in Japan were tested with three Philippine fungus strains and two Japanese ones in a greenhouse experiment. The three Philippine strains were chosen for their virulence to the tested varieties out of 80 isolates. The three strains were confirmed to have differential virulence to some selected resistance types in the Philippines. Against two Japanese strains, the resistance manifested by four upland varieties was very high in accordance with previously reported data. Although the infection was too severe to differentiate clearly the level of field resistance among ordinary lowland varieties, several varieties including Yamabiko and Kogane Nishiki were less severely infected than Norin 29 and Koshihikari in accordance with a general tendency in Japan. Against the Philippine strains, the level of the infection was, as a whole, lower than those caused by Japanese ones. However, the highly susceptible reaction of Norin 6 and Aichi Asahi indicated that the infection was severe enough to differentiate the field resistance among the entry. Next to Norin 6 and Aichi Asahi, Yamabiko and Kogane Nishiki were more susceptible than Koshihikari and Norin 29 which are generally among the most susceptible in the reaction to Japanese fungus strains. Inspection of lesion types on these varieties, when infected by the Philippine fungus strains, showed that the lesions on the leaves of Yamabiko and Kogane Nishiki were expanding ones with grayish green margin, while those on Norin 29 and Koshihikari were characterized by brownish margin. From the results it is proved that the field resistance which is conceived to be relatively stable to various strains of the fungus is ineffective to some exotic strains. Therefore, it should be considered that all of field, quantitative, partial or incomplete resistance is not necessarily non-specific, horizontal or general resistance.

Introduction

The varietal resistance to rice blast, *Pyricularia oryzae* Cav., has been divided into two categories, i. e., true resistance and field resistance (KIYOSAWA, 1970). The true resistance is a high level of resistance, while the field resistance is defined as a low level of resistance detected in the absence of true resistance gene(s).

Field resistance has been generally conceived as non-specific to fungus strain (NIIZEKI, 1967, SAKURAI, 1968, and SAKURAI and TORIYAMA, 1967). This view has been confirmed by some recent works. ASAGA and YOSHIMURA (1969) reported the order of field resistance

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among highly resistant or highly susceptible varieties was not affected by different fungus strains. EZUKA (1973) noticed that two derivatives from a Taiwan variety had high levels of field resistance to a number of Japanese fungus strains.

However, there are some contrasting views that the level of field resistance varies with different fungus strains. Some rice varieties with an extremely high level of field resistance against many races were found susceptible to some isolates (YUNOKI *et al.* 1970, and TORIYAMA 1971). YUNOKI *et al.* (1970) also reported that some varieties noted for their moderate field resistance showed a wide range of reaction to various fungus strains. They proposed to distinguish two types of field resistance, namely stable and variable ones.

Ou (1970) tested 63 Japanese varieties with known level of field resistance and known true resistance gene at a blast nursery at The International Rice Research Institute (IRRI) in the Philippines. According to him the results confirmed two points:

1) Many of such field-resistant varieties were completely killed by leaf blast, despite their moderate or high level of resistance in Japan. He argued that many of such field-resistant varieties did not have field resistance in the conventional sense, i. e., horizontal resistance. 2) Among the varieties with the same true resistance genes, their reactions were differentiated into susceptible or resistant ones depending on variety. He suggested that the different reactions might be caused by some other genes besides the known specific genes.

Regarding his first point, it should be noted that whether or not field resistance is 'horizontal' is a question to be answered through a specifically designed study. As for his second point, the possibility may not be denied that any true resistance gene which is idle for Japanese fungus races might have been in effect for Philippines fungus strains. If so, evaluation of field resistance would not have been possible in such a test.

The review of the arguments on the specificity of field resistance indicates the need of a well-conceived test to measure the extent to which field resistance is strain-specific. Ou's data suggest that the use of exotic fungus strains for Japanese varieties may clearly reveal the strain-specificity of field resistance. But an observation of varietal difference in a field test would not necessarily satisfy the essential requirement for the evaluation of field resistance, namely, the exclusion of any contribution by true resistance gene(s).

In the present study, specifically selected strains and varieties were used to avoid confusions mentioned above. And also an inoculation technique was applied in a greenhouse to test the field resistance of some Japanese varieties against Philippine and Japanese fungus strains.

Materials and Methods

Twenty four Japanese varieties with known levels of field resistance were chosen for the test.

Major portion of the varieties are derivatives of a cross between Norin 6 and Norin 8, as they represent a main trend of current varieties. Four upland varieties were included

for their extremely high level of field resistance in addition to a group of varieties noted for their field resistance. All the seeds were supplied by The Seed Storage Laboratory at National Institute of Agricultural Sciences (NIAS).

About 80 fungus strains were obtained by means of monoconidial isolation from blast-infected leaves which were collected at an upland blast nursery at IRRI in April, 1980. All the isolates were thereafter tested against 20 rice varieties including Kiyosawa's differential varieties (Kiyosawa, 1979) and some varieties and breeding lines selected at IRRI for representing major resistance types (Ikehashi, 1979). From the test three strains were chosen for their virulence to all the varieties except one (Fujisaka 5). The three strains were also confirmed to have different virulence to the selected IRRI breeding lines and varieties, so that they might belong to different races in the Philippines. They are designated hereafter as Ph 80-21-6 (isolated from IR 442-2-58), Ph 80-49-2 and Ph 80-49-3 (both from IR 24). Two Japanese fungus strains P-2b and Ai 73-134- z^+ were added for comparison. These two strains were virulent to all the varieties except Fujisaka 5 which manifests true resistance by a gene, *Pi-i*, to the strain, P-2b and all the three Philippine strains. Accordingly the reaction of this variety was excluded from statistical analyses.

Table 1. Densities of spores for spore suspension (10^4 /ml)

Isolates	Sept. 1	Date of inoculation		Average
		Oct. 24	Dec. 15	
Ai 73-134- z^+	31.5	28	17	25
P-2b	12	4.3	22.5	12.9
Ph 80-21-6	17	5.5	7.5	10.0
Ph 80-49-2	15	14	17.5	15.5
Ph 80-49-3	3	7.7	3	4.5

Notes : 1. Average of two or three counts for each inoculation.

2. A drop of wettable agent was added to the spore suspension, when the density of spore was less than 8×10^4 /ml.

The inoculation test was repeated three times from September to December in 1980 in a greenhouse at NIAS. The twenty four varieties were seeded in a wooden box. In each box, six to eight seedlings per variety were grown up to four or five leaf stage of the plant, when the seedlings were inoculated by means of spray of spore suspension of 20 ml per box. Two boxes were used for the inoculation with a strain. The density of the spore of the suspension was not uniform among the strains, and higher for Japanese strains than for Philippine ones due to differential sporulation ability (Table 1). The lesion development was recorded about 10 days after the inoculation on individual plant bases according to the system by Kiyosawa (1976).

Results

The reactions of the 24 varieties to each of the five fungus strains were averaged over the two trials each with one box, and subjected to variance analysis as a whole (Table 2), and separately according to the origin of the strains (Tables 3 and 4).

In each of the variance analyses, the variances due to the primary sources (varieties, replication and strains) are tested against the variances of the interaction between varieties and strains, because this interaction variance seemed relatively large with an adequate degree of freedom. With this procedure to calculate the F-values, throughout the three

Table 2. Analysis of variance for the field resistance of varieties to five strains of rice blast

Source of variance	SS	DF	MS	F V×R×S	F V×S
Variety	1419.5	22	64.5		4.07**
Replication	10.8	2	5.4		<1
Strain	683.1	4	170.8		10.76**
Var. × Rep.	133.1	44	3.03	1.84*	
Var. × Str.	698.1	88	7.9	4.81**	
Rep. × Str.	143.8	8	18.0	10.90**	
V. × R. × S.	291.0	176	1.65		

Notes : 1. F value for primary source of variance is calculated against the variance for variety × strain.

2. F value for the interaction of primary sources is calculated against the variance for var. × rep. × str.

*** : Significant at 5 or 1 percent level, respectively.

Table 3. Analysis of variance for the field resistance of 23 varieties to two Japanese strains

Source of variance	SS	DF	MS	F V×R×S	F V×S
Variety	918.0	22	41.7		18.3**
Replication	15.4	2	7.7		3.38
Strain	31.6	1	31.6		13.9**
Var. × Rep.	73.3	44	1.67	<1	
Var. × Str.	50.1	22	2.28	1.04	
Rep. × Str.	90.0	2	45.0	20.5**	
V. × R. × S.	96.3	44	2.19		

Note : F values are calculated by the same way as in Table 2.

*** : Significant at 5 or 1 percent level, respectively.

Table 4. Analysis of variance for the field resistance of 23 varieties to three Philippine strains

Source of variance	SS	DF	MS	F V×R×S	F V×S
Variety	978.6	22	44.5		11.4**
Replication	3.3	2	1.7		<1
Strain	32.5	2	16.3		4.18**
Var. × Rep.	119.1	44	2.7	2.01**	
Var. × Str.	170.6	44	3.9	2.91**	
Rep. × Str.	45.8	4	11.5	8.27**	
V. × R. × S.	117.8	88	1.34		

Note : F values are calculated by the same way as in Table 2.

*** : Significant at 5 or 1 percent level, respectively.

analyses the varietal differences and the difference due to the strains were confirmed to be statistically significant, at the same time the replications did not give significant difference.

The three interaction variances between the two primary sources of variances were significant in the variance analyses for all the strains (Table 2) and for the Philippine strains (Table 4). In the analysis for the Japanese strains the interaction variances were not significant except the one between replications and strains.

The variance analyses verified the significant differences among reactions due to the varieties and fungus strains. However, the significant interactions between replications and strains indicate a relatively large environmental errors which are related to various uncontrolled factors in measuring the field resistance. Therefore, our attention should be focused to apparently contrasting reactions of some varieties herewith by figuring all the data (Figs. 1 and 2).

Fig. 1. Varietal resistance of 24 Japanese rice varieties against two Japanese strains of rice blast fungus *Pyricularia oryzae* Cav.; P-2b (O) and Ai 73-134-z⁺ (X). Varietal names are listed below :

1. Norin 29	7. Koshijiwase	13. Ginga	19. Homare Nishiki
2. Koshihikari	8. Honenwase	14. Kinmaze	20. Sensho
3. Norin 8	9. Yamabiko	15. Syuho	20. Rikuto Norin 12
4. Norin 6	10. Suzuhara Mochi	16. Kogane Nishiki	21. Hatakogane
5. Nipponbare	11. Fujiminori	17. Toyonishiki	22. Rikuto N. Mochi 4
6. Norin 22	12. Aichi Asahi	18. Futaba	24. Fujisaka 5

The reactions of 24 varieties to Japanese strains are shown in Fig. 1. Of the reactions the resistance revealed by Fujisaka 5 indicates true resistance due to its *Pi-i* gene which is known to control the resistance to the strain P-2b and the three Philippine strains. Except that all the observed reactions were due to field resistance.

The resistance exhibited by four upland varieties (No. 20, 21, 22 and 23 in Fig. 1) was very high in accordance with previously reported results (ABE *et al.*, 1974). Although the infection was too severe to differentiate clearly the level of field resistance among ordinary lowland varieties, throughout the reactions to two Japanese fungus strains,

Fig. 2. Varietal resistance of 24 Japanese varieties against three Philippine strains of rice blast fungus; Ph 80-21-6 (x). Ph 80-49-2 (Δ) and Ph 80-49-3 (○). The code number for varietal names is the same as in Fig. 1.

Norin 22, Koshijiwase, Honenwase, Yamabiko and Toyonishiki (No. 6, 7, 8, 9 and 17, respectively) were less severely infected than Norin 29 and Koshihikari (No. 1 and 2). Six varieties (No. 10, 13, 15, 16, 18 and 19), which were bred out at a breeding station in a severe pressure of blast disease, namely Inahashi, exhibited a moderate level of field resistance.

Against the Philippine fungus strains the level of the infection is, as a whole, lower than those caused by Japanese fungus strains (Fig. 2). However, the clearly susceptible reaction by Norin 6 and Aichi Asahi (No. 4 and 12) suggested that the infection was severe enough to differentiate the field resistance among the varieties. Next to the two, Yamabiko and Kogane Nishiki (No. 9 and 16) were more susceptible than Koshihikari and Norin 29 which were among the most susceptible in Japan (EZUKA, 1972). The high susceptibility of Yamabiko and Kogane Nishiki to the Philippine strains is contrasting with their moderate resistance to Japanese fungus strains. Inspection of lesion types on these varieties confirmed the differential reaction further; the lesions on the leaves of Yamabiko and Kogane Nishiki when inoculated with Philippine fungus strains were expanding type with grayish green margin, while those on Norin 29 and Koshihikari were characterized by brownish margin.

The resistance of four upland varieties was found also effective against the Philippine fungus isolates, as that was to Japanese strains. But one of the upland varieties, Rikuto Norin 12 (No. 21), was less resistant than some of lowland varieties (for example, No. 7 and 8).

Discussion

Field resistance or quantitative resistance is generally conceived to be of a non-specific

nature, and often designated with such terms as horizontal, general or generalized resistance. However, increasing evidences are reported to argue that field resistance is specific to strains of causal organisms. In some cases of host pathogen relationship, a resistance which had been considered non-specific became recognized as specific (YUNOKI *et al.*, 1970, JOHNSON and TAYLOR, 1972, HAYES, 1973). PARLEVLIET and ZADOKS (1977) referred to many examples of minor genes for specific resistance. In other case, a true resistance gene with specific reaction was found to control field resistance after an appearance of a virulent mutant which overcame the specific resistance genes (MARTIN and ELLINGBOE, 1976, RILEY, 1973, KIYOSAWA, 1977). RILEY (1973) named such a resistance gene 'ghost gene'. In such a case monogenic field resistance should be of a specific nature.

Precise evaluation of the field resistance is not necessarily easy; it is possible only after classification of varieties based on their true resistance gene(s) (EZUKA *et al.*, 1969). Measuring the field resistance in field conditions is difficult, unless adequate information is available on the true resistance gene in the materials. Evaluation of field resistance for exotic varieties would especially difficult, because any unknown true resistance gene might be functional to exotic fungus strains, even if enough information is provided for effective genes to domestic fungus strains. Sometimes the field resistance would not be manifested fully, if the plants are exposed to too severe infection at early growth stage.

Ou (1979) tested 63 Japanese varieties with known level of field resistance at The International Rice Research Institute, and came to a conclusion that field resistance of the Japanese varieties did not work against Philippine strains of rice blast. But as a test for field resistance, there remain some questions in Ou's test; there might have been any unknown gene having affected the expression of the resistance, as he also assumed; and field resistance would not have been manifested fully at the early stage of the growth in that test.

The present study designed to meet the requirements for test of field resistance indicated that many of the tested varieties showed correlative reactions to the Philippine and Japanese strains, and that the field resistance of some varieties were in effect to exotic strains as well as to domestic one. At the same time it was clearly revealed that the field resistance of some varieties like Yamabiko and Kogane Nishiki was strain-specific; when infected by Japanese strains, they are more resistant than Koshihikari and Norin 29, which are among the most susceptible in Japan (EZUKA, *et al.*, 1969); but they are very susceptible to Philippine strains with far lower level of field resistance than that of Koshihikari and Norin 29. Therefore, their field resistance is strain-specific, and this fact seems to be revealed clearly with exotic fungus strains. Because field resistance is emphasized in the expectation of its stability against diverse fungus strains, further researches seem necessary to know the extent to which the resistance is strain-specific and to analyze the genetic bases for the resistance.

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フィリピンのいもち病菌系に対する日本の稲品種の 圃場抵抗性の特異性

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一般に圃場抵抗性はレースや菌系による変動が少ないとされ、いもち病抵抗性育種の主要な対象とされている。しかし圃場抵抗性がレースについて特異的であるとする報告もある。ここでは外国から得た菌系と日本の菌系を用いて、日本の品種の圃場抵抗性を調べた結果を報告する。

1980年4月にフィリピンにある国際稲研究所(IRRI)の葉いもち検定圃場から罹病葉を収集し、輸入した。これらの罹病葉から単孢子分離により、約80の菌株が分離された。これらの菌株は、清沢(1979)の判別品種と、IRRIで抵抗性の型が異なるとして選定された系統およびその他の計20品種に対する接種試験に供試された。その結果から、ここでは *Pi-a* を侵す3菌系を、IRRIの系統の抵抗性に判別力のあるものとして選定した。比較のため、日本のレースとして、P-2b および愛 73-134-*z*⁺ を供試した。

供試品種は、農林6号と同8号に関係のある品種群、愛知県の稲橋で育成された品種および陸稲などである。このうち藤坂5号では、愛 73-134-*z*⁺ 以外の菌系には真性抵抗性が働いていた。供試種子は農技研種子貯蔵管理室より得たものである。

接種試験は、1980年9月より12月までに3回実施した。第1回には本葉3葉展開時に、第2,3回には第4葉時に、常法によって得た孢子浮遊液を噴霧接種した。孢子濃度は、孢子形成の多い日本の菌系で高く、これによる発病程度も大きかった。なお孢子濃度の低い場合には展着剤を加えて調整した。各回の接種で、一菌系に2反復を供試し、接種約10日後に清沢(1979)の方法に準じて発病を記録した。

検定の結果から、両国の菌系に対する品種の圃場抵抗性にはある程度の共通性がみられた。すなわち陸稲は概して強いと判定された。日本の菌系に対しては、農林29号やコシヒカリが弱く、ヤマビコや黄金錦は、それらよりやや強いと見られた。フィリピンの菌系に対しては、農林6号、愛知旭、ヤマビコおよび黄金錦が弱かった。コシヒカリや農林29号などは、これらの品種より高い圃場抵抗性を示した。

ヤマビコと黄金錦は、日本の菌系には、周辺部が褐色の病斑を示したが、フィリピンの菌系には急性拡大型の病斑をコシヒカリと農林29号はその逆の反応を示し、とくに菌系によって圃場抵抗性が大きく変動するものと認められた。

一般に圃場抵抗性は菌系による特異性がないものとされているが、ここに認められた事実は、その考え方に再検討の余地があることを示している。