Modeling on the Race Frequency Change in a Host-Pathogen System with Genes for Resistance and Avirulence

Shigehisa KIYOSAWA* and Shun-ichi YABUKI**

* National Institute of Agricultural Sciences, Hiratsuka, Kanagawa 254

** Agricultural Research Institute of Kanagawa Prefecture, Hiratsuka, Kanagawa 254

In a host-pathogen system which includes four genotypes for true resistance, AB, A+, +B and ++, in a host population, and four genotypes (races) for avirulence, ab, a+, +b and ++, in an airborne pathogen population, we established equations for following the race frequency changes on a given host population. Here, A and B are resistance genes, and a and b are avirulence genes which specifically correspond to the respective resistance genes.

$$\begin{aligned} p_1^{(i)} &= \frac{p_1^{(i-1)} r_1 Q_4}{p_1^{(i-1)} r_1 Q_4 + p_2^{(i-1)} r_2 (Q_3 + Q_4) + p_3^{(i-1)} r_3 (Q_2 + Q_4) + p_4^{(i-1)} r_4}, \\ p_2^{(i)} &= \frac{p_2^{(i-1)} r_2 (Q_3 + Q_4)}{p_1^{(i-1)} r_1 Q_4 + p_2^{(i-1)} r_2 (Q_3 + Q_4) + p_3^{(i-1)} r_3 (Q_2 + Q_4) + p_4^{(i-1)} r_4}, \\ p_3^{(i)} &= \frac{p_3^{(i-1)} r_3 (Q_2 + Q_4)}{p_1^{(i-1)} r_1 Q_4 + p_2^{(i-1)} r_2 (Q_3 + Q_4) + p_3^{(i-1)} r_3 (Q_2 + Q_4) + p_4^{(i-1)} r_4}, \end{aligned}$$

and

$$p_4^{(i)} = \frac{p_4^{(i-1)} r_4}{p_1^{(i-1)} r_1 Q_4 + p_2^{(i-1)} r_2 (Q_3 + Q_4) + p_3^{(i-1)} r_3 (Q_2 + Q_4) + p_4^{(i-1)} r_4}.$$

where $p^{(i)}$ is the frequency of each race after the i -th generation, r is the multiplication rate of each race, and Q is the product of the percent of growing area (q) of a variety with a genotype for resistance and its field susceptibility (s). Subscripts, 1, 2, 3 and 4, correspond to genotypes (races) for avirulence, ab, a+, +b and ++, in the pathogen, and to genotypes for resistance, AB, A+, +B and ++, in the host, respectively. $p_1 + p_2 + p_3 + p_4 = 1$ and $Q_1 + Q_2 + Q_3 + Q_4 = 1$.

An equilibrium of race frequency is achieved under the following condition:

$$Q_4 = r_4/r_1, \quad Q_3 = r_4(1/r_2 - 1/r_1), \quad Q_2 = r_4(1/r_3 - 1/r_1),$$

and

$$Q_1 = 1 - r_4(1/r_2 + 1/r_3 - 1/r_1).$$

Introduction

It is well known that the genotype frequency for resistance in the host population influences the frequency of pathogenic races of airborne fungal pathogen (JOHNSON 1953, KIYOSAWA *et al.* 1975, WATSON 1970, WATSON and LUIG 1963). The difference of multiplication rates among races is also considered as an important factor affecting the race frequency (MODE 1958, VAN DER PLANK 1963). However, there is no study in which the rule for the change of race frequency depending upon genotype frequency in the host population is quantitatively expressed or formulated. This is partially due to the necessity of a long term to identify many isolates in relation to pathogenicity.

It is considerably difficult to find a special association of genotype for avirulence with multiplication ability which is closely related to stabilizing selection in the fungal population.

Received February 16, 1976

A question arises as to whether or not a slight difference of multiplication ability or fitness greatly influencing stabilizing selection during a long term can be experimentally detected. In other words, a slight difference of multiplication ability or fitness which is experimentally not detected might have a great influence on the race frequencies. It is important to estimate the difference of multiplication ability or fitness among genotypes for virulence capable of explaining the present relationship between race frequencies and genotype frequencies for resistance in the host population. For example, YABUKI and KIYOSAWA (1975) found in the rice-blast relationship (KIYOSAWA 1974) that there were $Av-a Av-k^+$, $Av-a^+ Av-k$ and $Av-a^+ Av-k^+$ races but not $Av-a Av-k$ race in Kanagawa Prefecture, Japan, where $Pi-a^+ Pi-k$, $Pi-a Pi-k^+$ and $Pi-a^+ Pi-k^+$ varieties were grown. Here, $Av-a^+ Av-k$ race shows a race of blast fungus which has a virulence allele $Av-a^+$ and an avirulence allele $Av-k$, and $Pi-a Pi-k^+$ variety shows a variety of rice carrying a resistance allele $Pi-a$ and a susceptibility allele $Pi-k^+$. The avirulence gene $Av-k$ corresponds specifically to the resistance gene $Pi-k$.

Generally, $Av-a Av-k^+$ and $Av-a^+ Av-k$ races are considered to evolve from $Av-a Av-k$ race by mutation. If so, why was the $Av-a Av-k$ race not found in Kanagawa Prefecture? This question stimulated the authors to begin this study.

The change of race frequency assuming that there is no difference of field resistance among genotypes for resistance and no difference of multiplication ability among races

Let us consider two resistance genes in the host, A and B, and two avirulence genes in the pathogen, a and b. There are four genotypes in the host, AB, A+, +B and ++, and four genotypes in the pathogen, ab, a+, +b and ++. Here, + means susceptibility allele in the host and virulence allele in the pathogen.

Table 1. Frequency of contacts between four genotypes for resistance in host population and four genotypes for avirulence in pathogen population

Host		Pathogen genotype and its frequency			
Genotype	Frequency	ab	a+	+b	++
		p_1	p_2	p_3	p_4
AB	q_1	R	R	R	S (p_4q_1)
A+	q_2	R	R	S (p_3q_2)	S (p_4q_2)
+B	q_3	R	S (p_2q_3)	R	S (p_4q_3)
++	q_4	S (p_1q_4)	S (p_2q_4)	S (p_3q_4)	S (p_4q_4)
Total		$p_1q_4 + p_2(q_3 + q_4) + p_3(q_2 + q_4) + p_4$			

If these genotypes are present in frequencies, p_1, p_2, p_3 and p_4 in the pathogen ($p_1 + p_2 + p_3 + p_4 = 1$) and q_1, q_2, q_3 and q_4 in the host ($q_1 + q_2 + q_3 + q_4 = 1$), relative frequencies of these genotypes in the next generation of vegetative reproduction of the pathogen are calculated as follows from Table 1.

The frequency of ab race in the next generation ($p_1^{(1)}$) is:

$$p_1^{(1)} = \frac{p_1q_4}{p_1q_4 + p_2(q_3 + q_4) + p_3(q_2 + q_4) + p_4(q_1 + q_2 + q_3 + q_4)}$$

$$= \frac{p_1 q_4}{p_1 q_4 + p_2(q_3 + q_4) + p_3(q_2 + q_4) + p_4} \quad (1)$$

In the same way,

$$p_2^{(1)} = \frac{p_2(q_3 + q_4)}{p_1 q_4 + p_2(q_3 + q_4) + p_3(q_2 + q_4) + p_4}, \quad (2)$$

$$p_3^{(1)} = \frac{p_3(q_2 + q_4)}{p_1 q_4 + p_2(q_3 + q_4) + p_3(q_2 + q_4) + p_4}, \quad (3)$$

$$p_4^{(1)} = \frac{p_4}{p_1 q_4 + p_2(q_3 + q_4) + p_3(q_2 + q_4) + p_4}. \quad (4)$$

After the second generation, the frequency of ab race becomes

$$p_1^{(2)} = \frac{p_1^{(1)} q_4}{p_1^{(1)} q_4 + p_2^{(1)}(q_3 + q_4) + p_3^{(1)}(q_2 + q_4) + p_4^{(1)}}.$$

As general equations, the frequencies of various races after the i -th generation are:

$$p_1^{(i)} = \frac{p_1^{(i-1)} q_4}{p_1^{(i-1)} q_4 + p_2^{(i-1)}(q_3 + q_4) + p_3^{(i-1)}(q_2 + q_4) + p_4^{(i-1)}}, \quad (5)$$

$$p_2^{(i)} = \frac{p_2^{(i-1)}(q_3 + q_4)}{p_1^{(i-1)} q_4 + p_2^{(i-1)}(q_3 + q_4) + p_3^{(i-1)}(q_2 + q_4) + p_4^{(i-1)}}, \quad (6)$$

$$p_3^{(i)} = \frac{p_3^{(i-1)}(q_2 + q_4)}{p_1^{(i-1)} q_4 + p_2^{(i-1)}(q_3 + q_4) + p_3^{(i-1)}(q_2 + q_4) + p_4^{(i-1)}}, \quad (7)$$

$$p_4^{(i)} = \frac{p_4^{(i-1)}}{p_1^{(i-1)} q_4 + p_2^{(i-1)}(q_3 + q_4) + p_3^{(i-1)}(q_2 + q_4) + p_4^{(i-1)}}. \quad (8)$$

Let us consider the change of frequency of each race. The frequency (p_1') of ab race after one vegetative generation is as follows from equation (1):

$$\begin{aligned} p_1' &= p_1 \frac{q_4}{q_4(p_1 + p_2 + p_3 + p_4) + p_2 q_3 + p_3 q_2 + p_4(q_1 + q_2 + q_3)} \\ &= p_1 \frac{q_4}{q_4 + p_2 q_3 + p_3 q_2 + p_4(q_1 + q_2 + q_3)}. \end{aligned} \quad (9)$$

Here, p_2, p_3, p_4, q_1, q_2 or q_3 is always equal to or greater than 0. If $p_2 = p_3 = p_4 = 0$,

$$p_1' = p_1.$$

Accordingly, the frequency of ab race does not change. From equation (9),

$$p_1' = p_1 \frac{q_4}{q_4 + q_3(p_2 + p_4) + q_2(p_3 + p_4) + q_1 p_4}. \quad (9')$$

Accordingly, when $q_1 = q_2 = q_3 = 0$, $p_1' = p_1$.

Also in this case, the frequency of ab race does not change.

Similarly,

$$\begin{aligned} p_2' &= \frac{p_2(q_3 + q_4)}{p_4 + p_3(q_2 + q_4) + p_2(q_3 + q_4) + p_1 q_4} \\ &= p_2 \frac{q_3 + q_4}{q_4(p_4 + p_3 + p_2 + p_1) + q_3[p_2 + p_4 + p_1 + p_3 - (p_1 + p_3)] + q_2(p_3 + p_4) + q_1 p_4} \\ &= p_2 \frac{q_3 + q_4}{q_3 + q_4 - q_3(p_1 + p_3) + q_2(p_3 + p_4) + q_1 p_4}. \end{aligned} \quad (10)$$

Here, $q_3(p_1 + p_3)$ is an increasing factor, and $q_2(p_3 + p_4) + q_1 p_4$ is a decreasing factor of a + race. If $q_3(p_1 + p_3) > q_2(p_3 + p_4) + q_1 p_4$, $p_2' > p_2$, that is, the frequency of a + race increases.

and if $q_3(p_1+p_3) < q_2(p_3+p_4) + q_1p_4$, $p_2' < p_2$, showing the usual decrease of the frequency of a+ race. Of course, when $q_3(p_1+p_3) = q_2(p_3+p_4) + q_1p_4$, the frequency of the a+ race is constant.

For the +b race frequency in the pathogen population,

$$p_3' = p_3 \frac{q_2 + q_4}{q_2 + q_4 - q_2(p_1 + p_2) + q_3(p_2 + p_4) + q_1p_4}. \quad (11)$$

The +b race frequency tends to increase with an increase of the percent of growing area of the A+ genotype of the host and to decrease with a frequency increase of +B genotype or AB genotype of the host or both.

For the ++ race frequency,

$$\begin{aligned} p_4' &= p_4 \frac{1}{p_4 + p_3(q_2 + q_4) + p_2(q_3 + q_4) + p_1q_4} \\ &= p_4 \frac{1}{p_4 + p_3[1 - (q_1 + q_3)] + p_2[1 - (q_1 + q_2)] + p_1[1 - (q_1 + q_2 + q_3)]} \\ &= p_4 \frac{1}{1 - [q_1(p_1 + p_2 + p_3) + q_2(p_1 + p_2) + q_3(p_1 + p_3)]}. \end{aligned} \quad (12)$$

when $p_1 = p_2 = p_3 = 0$, or $q_1 = q_2 = q_3 = 0$,

$$p_4' = p_4$$

Therefore, the ++ race frequency does not change. If $q_1(p_1 + p_2 + p_3)$, $q_2(p_1 + p_2)$, $q_3(p_1 + p_3)$, $p_1(q_1 + q_2 + q_3)$, $p_2(q_1 + q_2)$ or $p_3(q_1 + q_3)$ is over 0, the ++ race frequency increases.

It has been frequently reported that the frequency of virulent races to a variety carrying specific resistance gene decreases after removing the variety from the area (IWATA and YAOITA, Unpublished, JOHNSON 1953, WATSON and LUIG 1963). It is of great interest to know the frequency change of the virulent races after removing the resistant variety assuming there is no racial difference of multiplication ability and no varietal difference of field resistance. For example, let us remove AB and A+ genotypes from the host population. In this case, q_1 and q_2 are 0. From equation (9'),

$$p_1' = p_1 \frac{q_4}{q_4 + q_3(p_2 + p_4)}. \quad (13)$$

If q_3 is not 0, that is, +B genotype of the host is growing, the ab race frequency decreases.

From equations (10), (11) and (12),

$$p_2' = p_2 \frac{q_3 + q_4}{q_3 + q_4 - q_3(p_1 + p_3)}, \quad (14)$$

$$p_3' = p_3 \frac{q_4}{q_4 + q_3(p_2 + p_4)}, \quad (15)$$

and

$$p_4' = p_4 \frac{1}{1 - q_3(p_1 + p_3)}. \quad (16)$$

From these equations, we can see that the frequencies of a+ and ++ races increase and one of +b race decreases. The frequencies of a+ and ++ races become constant after ab and +b races decrease to 0.

Summarizing these results, the frequencies of ab, a+, +b races decrease very quickly in

the presence of A and B genes, and the $a+$ genotype frequency in the pathogen population does not decrease after removing the B gene from the host population. These results do not agree with many observations.

For example, YABUKI and KIIYOSAWA (1975) tested pathogenicity of about 250 isolates of blast fungus using KIIYOSAWA's differential rice varieties (KIIYOSAWA 1974). These fungus isolates were collected from 17 places in representative rice growing areas in Kanagawa Prefecture. In this prefecture, rice varieties Nippon-bare and Kusabue were grown in 33.8 % and 26.7% of rice growing area, respectively. The blast fungus was isolated from the neck of the ear usually of the two varieties and frequently of an additional variety which was grown in a large area in its location or was severely diseased. Specialization of races was found for only Kusabue (carrying the resistance gene $Pi-k$), K2 ($Pi-k^b$, an allele of $Pi-k$ locus), K3 ($Pi-k^h$, an allele of $Pi-k$ locus), Aichi Asahi ($Pi-a$) and Fujisaka 5 ($Pi-i$) for which only three virulent isolates were found.

In all, three genotypes (races) of blast fungus, $Av-a Av-k^+$, $Av-a^+ Av-k$ and $Av-a^+ Av-k^+$

Table 2. Estimation of race frequencies of blast fungus in Kanagawa Prefecture in 1974

Location	Variety	Genotype (race) of isolates		
		$Av-a^+ Av-k$	$Av-a Av-k^+$	$Av-a^+ Av-k^+$
Yokohama	Kusabue	0	0.90	0.10
	Nippon-bare	0.19	0.69	0.12
	Total	0.15	0.75	0.10
Atsugi	Kusabue	0	0.84	0.16
	Nippon-bare	0.50	0.10	0.40
	Tsukuba-nishiki	0	0	1.00
	Total	0.15	0.55	0.30
Hiratsuka	Kusabue	0	0.93	0.07
	Nippon-bare	0.42	0.54	0.04
	Total	0.17	0.77	0.06
Isehara	Kusabue	0	0.90	0.10
	Nippon-bare	0.13	0.55	0.32
	Total	0.04	0.79	0.17
Ashigara-Kami	Kusabue	0	1.00	0
	Nippon-bare	0.11	0.84	0.05
	Total	0.05	0.93	0.02
Odawara	Kusabue	0	1.00	0
	Nippon-bare	0.15	0.81	0.04
	Total	0.01	0.99	0
Kanagawa Prefecture	Kusabue	0	0.95	0.05
	Nippon-bare	0.26	0.56	0.18
	Total	0.10	0.80	0.10

(YABUKI and KIIYOSAWA, 1975)

were predominantly found. Here, $Av-a$ and $Av-a^+$ are avirulence and virulence alleles corresponding to resistance gene $Pi-a$. The frequency of the i -th race (R_i) was calculated by:

$$R_i = \frac{\sum_j R_{ij} A_j S_j}{\sum_j A_j S_j},$$

where R_{ij} is the number of the i -th race collected on the j -th variety, and A_j and S_j are growing area and disease severity of the j -th variety, respectively. Thus, Table 2 was obtained.

In Kanagawa Prefecture, there is no large change on percent of growing area of varieties with various genotypes for resistance: Kusabue has a resistance gene ($Pi-k$) (KIIYOSAWA 1974) and Nippon-bare is in mixture of $Pi-a$ and $Pi-a^+$ (ASAGA and YOSHIMURA 1973, EZUKA *et al.* 1969, YABUKI and KIIYOSAWA 1975). A large difference between the observed

frequencies and the calculation under the assumption stated above is found. According to the calculation, the ++ race predominates after several vegetative generations of the pathogen. However, the ++ race frequency is considerably small in the observed frequencies. This may indicate that the assumption is not valid.

The observed changes of the frequency of virulent race after removing resistant variety or varieties (JOHNSON 1953, WATSON and LUIG 1963) are not consistent with the calculation. This also suggests that the assumption is not valid.

The race frequency change under the assumption where field resistance and multiplication ability are dependent upon the genotypes for true resistance and avirulence

It is well known that a variety developed as a highly resistant variety becomes more highly susceptible than native varieties a few years after the release of the resistant variety (KIYOSAWA 1965, VAN DER PLANK 1963, WATSON and LUIG 1963). The phenomena are called Vertifolia effect (VAN DER PLANK 1963). The explanation is that a variety with true resistance sometimes has a weaker field resistance or higher field susceptibility (KIYOSAWA 1965, VAN DER PLANK 1963).

Let us incorporate a difference of field susceptibility among genotypes for resistance into the model in Table 1. The degree of field susceptibility is given as s_1, s_2, s_3 and s_4 for AB, A+, +B and ++ genotypes for resistance, respectively.

VAN DER PLANK (1963, 1968) indicated that there is a difference of multiplication ability or fitness between fungus strains which are associated with genotypes for virulence. He mentioned that an unnecessary virulence gene reduces the fitness to survival. Reports suggesting the presence of such a phenomenon have also been found in blast disease (SHINDO 1973, YAMADA and IWANO 1972). Giving factors on field susceptibility (s_1, s_2, s_3 and s_4) and on multiplication ability or fitness (r_1, r_2, r_3 and r_4) to Table 1, Table 3 is obtained.

Table 3. Frequency of contacts between four resistance genotypes with different field susceptibility in host population and four avirulence genotypes with different multiplication ability in pathogen population

Host		Pathogen genotype and its frequency and multiplication ability			
Genotype	Frequency & field susceptibility	ab	a+	+b	++
		p_1r_1	p_2r_2	p_3r_3	p_4q_4
AB	q_1s_1	R	R	R	S ($p_4r_4q_1s_1$)
A+	q_2s_2	R	R	S ($p_3r_3q_2s_2$)	S ($p_4r_4q_2s_2$)
B+	q_3s_3	R	S ($p_2r_2q_3s_3$)	R	S ($p_4r_4q_3s_3$)
++	q_4s_4	S ($p_1r_1q_4s_4$)	S ($p_2r_2q_4s_4$)	S ($p_3r_3q_4s_4$)	S ($p_4r_4q_4s_4$)

Putting

$$\frac{q_1 s_1}{q_1 s_1 + q_2 s_2 + q_3 s_3 + q_4 s_4} = Q_1,$$

$$\frac{q_2 s_2}{q_1 s_1 + q_2 s_2 + q_3 s_3 + q_4 s_4} = Q_2,$$

$$\frac{q_3 s_3}{q_1 s_1 + q_2 s_2 + q_3 s_3 + q_4 s_4} = Q_3,$$

and

$$\frac{q_4 s_4}{q_1 s_1 + q_2 s_2 + q_3 s_3 + q_4 s_4} = Q_4,$$

$$Q_1 + Q_2 + Q_3 + Q_4 = 1.$$

In the same way as used to get equations (1) to (4),

$$p_1' = p_1 \frac{r_1 Q_4}{p_1 r_1 Q_4 + p_2 r_2 (Q_3 + Q_4) + p_3 r_3 (Q_2 + Q_4) + p_4 r_4}, \quad (17)$$

$$p_2' = p_2 \frac{r_2 (Q_3 + Q_4)}{p_1 r_1 Q_4 + p_2 r_2 (Q_3 + Q_4) + p_3 r_3 (Q_2 + Q_4) + p_4 r_4}, \quad (18)$$

$$p_3' = p_3 \frac{r_3 (Q_2 + Q_4)}{p_1 r_1 Q_4 + p_2 r_2 (Q_3 + Q_4) + p_3 r_3 (Q_2 + Q_4) + p_4 r_4}, \quad (19)$$

and

$$p_4' = p_4 \frac{r_4}{p_1 r_1 Q_4 + p_2 r_2 (Q_3 + Q_4) + p_3 r_3 (Q_2 + Q_4) + p_4 r_4}. \quad (20)$$

Let us consider the condition of an equilibrium of race frequencies. In equation (17), if

$$r_1 Q_4 = p_1 r_1 Q_4 + p_2 r_2 (Q_3 + Q_4) + p_3 r_3 (Q_2 + Q_4) + p_4 r_4, \quad (21)$$

$p_1' = p_1$. Accordingly, the frequency of ab race does not vary with generations. Similarly, the conditions for constancy of frequencies of other three races are

$$r_2 (Q_3 + Q_4) = p_1 r_1 Q_4 + p_2 r_2 (Q_3 + Q_4) + p_3 r_3 (Q_2 + Q_4) + p_4 r_4, \quad (22)$$

$$r_3 (Q_2 + Q_4) = p_1 r_1 Q_4 + p_2 r_2 (Q_3 + Q_4) + p_3 r_3 (Q_2 + Q_4) + p_4 r_4, \quad (23)$$

and

$$r_4 = p_1 r_1 Q_4 + p_2 r_2 (Q_3 + Q_4) + p_3 r_3 (Q_2 + Q_4) + p_4 r_4. \quad (24)$$

Therefore, $r_1 Q_4 = r_2 (Q_3 + Q_4) = r_3 (Q_2 + Q_4) = r_4$ are the conditions for constancy or equilibrium of race frequencies. From this,

$$Q_4 = \frac{r_4}{r_1}, \quad (25)$$

$$Q_3 = r_4 \left(\frac{1}{r_2} - \frac{1}{r_1} \right), \quad (26)$$

$$Q_2 = r_4 \left(\frac{1}{r_3} - \frac{1}{r_1} \right), \quad (27)$$

and

$$Q_1 = 1 - r_4 \left(\frac{1}{r_2} + \frac{1}{r_3} - \frac{1}{r_1} \right). \quad (28)$$

This indicates that we can get the values of Q_1, Q_2, Q_3 and Q_4 required for equilibrating the race frequencies by measuring the multiplication rate of each race on a variety with no resistance gene.

LEONARD (1969) proposed a method to determine the desired proportion of susceptible

varieties from the experimentally determined value for $1-s$, the difference in reproductive rates for races virulent and avirulent, respectively, on varieties with resistance gene(s). The equation used by him was in our notation

$$\frac{p_1'}{p_1} = (1-s) \frac{p_2'}{p_2}.$$

At an equilibrium,

$$\left(\frac{p_1'}{p_1} = \frac{p_2'}{p_2} = 1 \right), 1-s = \frac{m_0}{m_0+m_a}.$$

Here, p_1 equals the proportion of biotypes virulent only on susceptible varieties, p_2 equals the proportion of biotypes virulent on varieties with the A gene in the mixture of both biotypes, and m_0 and m_a are the proportions of susceptible plants and of plants with the A gene for resistance in the host mixture, respectively. In the equation, $m_0/(m_0+m_a)$ is the proportion of susceptible plants required to get $p_1'/p_1 = p_2'/p_2 = 1$ in which an equilibrium of the frequencies of both biotypes is achieved.

The similar relationships are obtained from equations (17) to (20) for the four genotypes (races) in our system.

$$\frac{p_1'}{p_1 r_1 Q_4} = \frac{p_2'}{p_2 r_2 (Q_3 + Q_4)} = \frac{p_3'}{p_3 r_3 (Q_2 + Q_4)} = \frac{p_4'}{p_4 r_4}.$$

Hence,

$$\frac{p_1'}{p_1} = \frac{r_1}{r_2} \frac{Q_4}{(Q_3 + Q_4)} \frac{p_2'}{p_2}.$$

At an equilibrium ($p'/p_1 = p_2'/p_2 = 1$),

$$\frac{r_2}{r_1} = \frac{Q_4}{Q_3 + Q_4}$$

In the same way,

$$\begin{aligned} \frac{p_1'}{p_1} &= \frac{r_1}{r_3} \frac{Q_4}{(Q_2 + Q_4)} \frac{p_3'}{p_3}, & \frac{r_3}{r_1} &= \frac{Q_4}{Q_2 + Q_4}, \\ \frac{p_1'}{p_1} &= \frac{r_1}{r_4} \frac{Q_4}{(Q_1 + Q_2 + Q_3 + Q_4)} \frac{p_4'}{p_4}, & \frac{r_4}{r_1} &= \frac{Q_4}{Q_1 + Q_2 + Q_3 + Q_4} = Q_4. \\ \frac{p_2'}{p_2} &= \frac{r_2}{r_3} \frac{(Q_3 + Q_4)}{(Q_2 + Q_4)} \frac{p_3'}{p_3}, & \frac{r_3}{r_2} &= \frac{Q_3 + Q_4}{Q_2 + Q_4}, \end{aligned}$$

and so on. These equations are essentially the same as that of LEONARD, except that the difference of field susceptibility among genotypes for true resistance is taken into consideration in this paper. Also from these equations, equations (25) to (28) are obtained.

The relationships between r 's and Q 's under an equilibrium condition are shown in Fig. 1 as an instance. Here, the calculations were performed under the assumption, $r_1/r_4 = (r_2/r_4)^2 = r_2 r_3 / r_4^2$.

The figure reveals that an equilibrium is never achieved if $r_1 = r_2 = r_3 = r_4$. Furthermore, if r_2 or r_3 is not much larger than r_4 , a considerably large proportion of ++ plants is necessary to achieve an equilibrium of race frequencies. Protection of the crop from diseases by mixing various genotypes for true resistance depends on the pleiotropic function of avirulence gene to increase multiplication ability. Such a function of avirulence gene

Fig. 1. Relationship between relative multiplication rate of races and percent growing areas of genotypes for resistance required for equilibrium of race frequency

causes the stabilizing selection in pathogen population. Thus, fungus strains carrying an avirulence gene remain in relatively high proportion in spite of their survival disadvantage on resistant plants. However, the amount of data is not sufficient to support the existence of stabilizing selection. It is first necessary to know the effect of avirulence gene on multiplication rate.

In this paper, the change of race frequency was considered in a host-pathogen system with two resistance genes in the host and two avirulence genes in the pathogen corresponding

specifically to the two genes for resistance. A similar method can be applied to a host-pathogen system with 3 or more gene pairs for resistance and avirulence.

The interpretation on the race frequency change of blast fungus observed in Kanagawa Prefecture by YABUKI and KIYOSAWA (1975) which became a starting point of this research will be discussed in the following paper.

Literature Cited

- ASAGA, K. and S. YOSHIMURA 1973. Change of disease severity with races and isolates. Basic Studies on Breeding Measures to Counter Exposed Outbreak of Blast Epidemics in Resistant Rice Varieties. Min. Agr. Forest. Fish. Council, Tokyo, 126~136. (In Japanese)
- EZUKA, A., T. YUNOKI, Y. SAKURAI, H. SHINODA and K. TORIYAMA 1969. Studies on the varietal resistance to rice blast. 1. Tests for genotype of "true resistance". Bull. Chugoku Agr. Exp. Sta. **E4**: 1~31. (In Japanese)
- IWATA, K. and Y. YAOITA. Unpublished.
- JOHNSON, T. 1953. Variation in the rusts of cereals. Biol. Rev. **28**: 105~157.
- KIYOSAWA, S. 1965. Ecological analysis on breakdown of resistance in resistant varieties and breeding counterplan against it. Nogyo Gijutsu (Agr. Tech.) **20**: 465~470, 510~512. (In Japanese)
- KIYOSAWA, S. 1966. On spontaneous mutation of pathogenicity of the blast fungus. Shokubutsu Boeki (Plant Prot.) **20**: 159~162. (In Japanese)
- KIYOSAWA, S. 1974. Studies on genetics and breeding of blast resistance in rice. Misc. Publ. Natl. Inst. Agr. Sci. **D1**: 1~58.
- KIYOSAWA, S., K. KUSHIBUCHI and S. WATANABE 1975. Breeding for blast resistance of rice and basic studies for it. —Present status and problems. Nogyo oyobi Engei (Agr. Hort.) **50**: 25~30, 258~262, 377~380, 629~635. (In Japanese)
- LEONARD, K. J. 1969. Factors affecting rates of stem rust increase in mixed plantings of susceptible and resistant oat varieties. Phytopathology, **59**: 1845~1850.
- MODE, C. J. 1958. A mathematical model for the co-evolution of obligate parasites and their hosts. Evolution, **12**: 158~165.
- SHINDO, K. 1973. Change of disease severity of rice varieties grown in seedling cases by different isolates belonging to T race of blast fungus. Basic Studies on Breeding Measures to Counter

- Exposive Outbreak of Blast Epidemics in Resistant Rice Varieties. Min. Agr. Forest. Fish. Council. Tokyo, 109~110. (In Japanese)
- VAN DER PLANK, J. E. 1963. Plant Diseases: Epidemics and Control. Academic Press, New York and London, pp. 349.
- VAN DER PLANK, J. E. 1968. Disease Resistance in Plants. Academic Press, New York and London. pp. 206.
- WATSON, I. A. 1970. Changes in virulence and population shifts in plant pathogens. Ann. Rev. Phytopath. 209~230.
- WATSON, I. A. and N. H. LUIG 1963. The classification of *Puccinia graminis* var. *tritici* in relation to breeding resistant varieties. Proc. Linn. Soc. N. S. W. 88 : 235~258.
- YABUKI, S. and S. KIYOSAWA 1975. Identification, distribution and frequency of races of blast fungus in Kanagawa in 1974. Researches on Actual Condition of Severe Outbreak of Rice Blast. Kanagawa Prefecture, 53~63. (In Japanese)
- YAMADA, M. and Y. IWANO 1972. Remarkable changes of race population of rice blast fungus in Niigata Prefecture. Joint Work on the Race of Blast Fungus, *Pyricularia oryzae* (Fascicle 3). Special Report on the Forecasting of Occurrence of the Disease and Insect Pest. 24 : 99~101. (In Japanese)

抵抗性と非病原性遺伝子をもつ「宿主-病原菌」系の中における レース頻度の変化に関するモデル作成

清沢 茂久*・矢吹 駿一**

(*農業技術研究所・**神奈川県農業総合研究所)

宿主集団における4つの真性抵抗性遺伝子型 AB, A+, +B と ++ と空気伝染性病原菌集団の4つの非病原性に関する遺伝子型 ab, a+, +b と ++ をもつ「宿主・病原菌」系において, 任意の宿主集団上でのレース頻度の変化を推定するための方程式を作成した。AとBは抵抗性遺伝子, aとbはこの抵抗性遺伝子に特異的に対応する非病原性遺伝子である。

$$\begin{aligned}
 p_1^{(i)} &= \frac{p_1^{(i-1)}Q_4}{p_1^{(i-1)}r_1Q_4 + p_2^{(i-1)}r_2(Q_3+Q_4) + p_3^{(i-1)}r_3(Q_2+Q_4) + p_4^{(i-1)}r_4}, \\
 p_2^{(i)} &= \frac{p_2^{(i-1)}r_2(Q_3+Q_4)}{p_1^{(i-1)}r_1Q_4 + p_2^{(i-1)}r_2(Q_3+Q_4) + p_3^{(i-1)}r_3(Q_2+Q_4) + p_4^{(i-1)}r_4}, \\
 p_3^{(i)} &= \frac{p_3^{(i-1)}r_3(Q_2+Q_4)}{p_1^{(i-1)}r_1Q_4 + p_2^{(i-1)}r_2(Q_3+Q_4) + p_3^{(i-1)}r_3(Q_2+Q_4) + p_4^{(i-1)}r_4}, \\
 p_4^{(i)} &= \frac{p_4^{(i-1)}r_4}{p_1^{(i-1)}r_1Q_4 + p_2^{(i-1)}r_2(Q_3+Q_4) + p_3^{(i-1)}r_3(Q_2+Q_4) + p_4^{(i-1)}r_4},
 \end{aligned}$$

ここで $p^{(i)}$ は i 世代後のそれぞれのレースの頻度であり, r はそれぞれのレースの増殖率, Q はある抵抗性遺伝子型をもつ品種の作付面積率 (q) とその圃場罹病性 (s) の積である。下付きの数字 1, 2, 3, 4 は病原菌の非病原性遺伝子型 ab, a+, +b, ++ と, 宿主の抵抗性遺伝子型 AB, A+, +B, ++ に相当する。 $p_1+p_2+p_3+p_4=1$, $Q_1+Q_2+Q_3+Q_4=1$ である。

次の条件の下でレース頻度は平衡に達する。

$$\begin{aligned}
 Q_4 &= \frac{r_4}{r_1} \\
 Q_3 &= r_4 \left(\frac{1}{r_2} - \frac{1}{r_1} \right) \\
 Q_2 &= r_4 \left(\frac{1}{r_3} - \frac{1}{r_1} \right) \\
 Q_1 &= 1 - r_4 \left(\frac{1}{r_2} + \frac{1}{r_3} - \frac{1}{r_1} \right).
 \end{aligned}$$