病害防除のための抵抗性品種混合の効果に関する理論的研究

誌名	日本植物病理學會報 = Annals of the Phytopathological Society of Japan
ISSN	00319473
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発行元	日本植物病理學會
巻/号	38巻1号
掲載ページ	p. 41-51
発行年月	1972年1月

日植病報 38: 41-51 (1972)
Ann. Phytopath. Soc. Japan 38: 41-51 (1972)

A Theoretical Evaluation of the Effect of Mixing Resistant Variety with Susceptible Variety for Controlling Plant Diseases

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清沢茂久*・塩見正衛**：病害防除のための抵抗性品種混合の効果に関する理論的研究

Abstract

In order to examine the effectiveness of use of multiline variety system, simulations of disease increase in the pure stand of susceptible variety and in the mixed stand of susceptible and resistant varieties were made by following the dispersal nature of pathogens.

Dispersal distributions of various pathogens were confirmed to fit the equation $y=\beta e^{-\alpha d}$, where y is the number of spores or lesions on a plant, d is distance in meter, and α and β are constant for dispersal gradient and the number of lesions on the source plants, respectively.

When the distance between plants is taken as a unit of distance, if α is less than 0.2 the effect to prevent the disease increase of mixture of resistant plants in susceptible population at a rate of 1 : 1 can be expressed by the Leonard's equation, $y'/y_0=m^n \times (y/y_0)$. The effect of mixing resistant plants decreases in α values over 0.2.

Double or multiple infection and the decrease of healthy area of susceptible plants are presumed to play an important role in flattening of dispersal distribution curve in the actual field as well as contamination from outside sources and the increase of infection generation as pointed out by Cammack. (Received July 22, 1971)

Introduction

Since an encounter with the breakdown of resistance of varieties which were developed for the disease resistance, the efforts of breeders in each country have been made to search how effectively to use resistance genes. Thus, the multiline variety system was prepared as a possible use of resistance genes for controlling diseases[1]. However, there are no theoretical studies on the effect of the multiline variety, except Leonard's reports[8,9,10]. The present paper is prepared based on the thought that the usefulness of the multiline variety can be theoretically criticized by following the dispersal nature of the pathogens.

The choice of a dispersal model

There are many investigations on the dispersal of pathogens, and many of them were collected by Gregory[4]. It is well known that the distribution of spores of pathogens gradually decreases from an inoculum source to every direction. Up to date, a few mathematical models were applied for the dispersal distribution.

$$y=\frac{a}{d^b}, \quad \text{(Gregory, 1968)} \qquad (1)$$

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$$y=\frac{b(1+a)^2}{(d+a)^2}, \quad \text{(Wilson and Baker, 1946)} \qquad (2)$$

$$s(x,y,z)=\frac{2Q}{C_yC_zux^{2-n}}\exp\left[-x^{n-2}\left(\frac{y^2}{C_y{}^2}+\frac{z^2}{C_z{}^2}\right)\right]. \quad \text{(Schrödter, 1960)} \qquad (3)$$

Here, y and d are the number of lesions and the distance from the inoculum plant, respectively, with the exception of equation (3). And, a and b are constants. Equation (3) shows the turbulent dispersal of spores in three dimentions, based on the theory of turbulent diffusion. This equation is too complicated to apply to the simulation of a disease increase, and three dimentional distribution is not necessary in considering the simulation.

In equation (1), the number of lesions on the inoculum plant is calculated to be infinite after each infection generation. In actual infection, the number of lesions on the source plant is not infinite and it is essential for the simulation to precisely estimate the increase of lesions on source plants. Therefore, it is not suitable to apply equation (1) to the simulation of the disease increase.

Equation (2) does not have the defect seen in equation (1), but this equation is also rather complex. Curves drawn by equation (2) can similarly be drawn by the following equation,

$$y=\beta e^{-\alpha d}=a\gamma e^{-\alpha d}, \qquad (4)$$

where α is the constant determining the dispersal gradient, a is the number of initial susceptible type lesions on the initial source plant, and β is the number of lesions on the initial source plant after the first infection cycle.

Equation (4) has more well-known mathematical natures than equation (2). Therefore, equation (4) may be more convenient to be used for the simulation than equation (2).

In order to know whether or not the dispersals of various pathogens fit equation (4), regression coefficients (α) and coefficients of determination (r^2) were calculated on the dispersals of spores of various pathogens collected by Gregory[4]. The results (Table 1) show that most of the calculations agree with equation (4). Therefore, equation (4) will be used for the simulation of disease increase.

Disease increase in pure stand of susceptible plants

Now, let us consider susceptible plants in a row where an inoculum plant with some susceptible type lesions is planted in the center. From the inoculum plant, spores are dispersed according to equation (4). In this equation, the number of susceptible type lesions formed on the inoculum plant after the first infection is represented by β; $y=\beta$, when $d=0$.

In equation (4), the total number of lesions formed on the susceptible plants in one row in the field is expressed by

$$\sum_{d=0}^{\infty} y_d=\beta+2\beta\sum_{d=1}^{\infty}e^{-\alpha d}=\beta\left(1+2\sum_{d=1}^{\infty}e^{-\alpha d}\right), \qquad (5)$$

where $\beta(=\beta e^{-0\alpha})$ is the number of lesions on the initial inoculum plant and $2\beta\sum_{d=1}^{\infty}e^{-\alpha d}$ is the total number of lesions on plants on both sides of the inoculum plant. In this paper, the dispersals of pathogens are compared among infection systems with the same infection rate and different dispersal gradients.

First, the values obtained by Yanagita and Shindo (unpublished) were used for γ and β of equation (4). They conducted an experiment on the dispersal or disease increase of rice blast in a field where susceptible variety was planted in only one row in resistant variety. At one end of this row diseased plant was transplanted. And, the number of susceptible type

Table 1. Dispersal gradients of spores or lesions of various pathogens

Crop plant	Pathogen		α[a]	β[a]	r^2[b]	Literature
Pinus	*Cronartium ribicola*		0.1962	11.928	0.6648	Buchanan & Kimmey[2], 1938
		[c]	0.617	68.83	0.9498	
Potato	*Phytophthora infestans*	Focus 1	5.132	323.6	0.9520	Limasset[11], 1939
		Focus 2	2.590	16.70	0.8975	
Onion	Downy mildew		0.0192	819.1	0.9926	Newhall[12], 1938
		[c]	0.0278	1442.5	0.9289	
Tulip plant	*Botrytis tulipae*	Bed 1	8.294	20.96	0.9942	Wallace[18], 1934
		Bed 2	3.482	33.49	0.8631	
Wheat	*Cercosporella herpotrichoides*		0.1062	59.05	0.6614	Oort[13], 1936
		[c]	0.1835	79.69	0.6958	
	Puccinia graminis	Aeciospore	2.594	314610	0.9905	Lambert[7], 1929
Agropyron repens	*Puccinia graminis*		1.769	620.99	0.8358	Johnson & Dickson[6], 1919
Wheat	*Ustilago tritici*	North-east	0.1913	104.4	0.7422	Oort[14], 1940
		South-east	0.0680	20.11	0.7109	
		Location 2	0.6544	1035.0	0.9044	
Barley	Powdery mildew	Variety 1	0.5190	179.8	0.8672	Pape & Rademacher[15], 1934
		Variety 2	0.3497	354.4	0.8335	
		Location 2	0.0178	145.6	0.7354	
Rice	*Pyricularia oryzae* (Spore)	1958	0.2954	2501.4	0.8049	Suzuki[17], 1964
		1959	0.3182	1559.2	0.8380	
		1960	0.3629	3798.4	0.6923	
		1961	0.3249	1197.3	0.6158	
		1962	0.3224	807.9	0.5998	
		1963 (South)	0.2257	1459.4	0.6357	
		1963 (North)	0.3410	1777.0	0.6767	
		1963 (East)	0.4824	2205.0	0.7179	
		1963 (West)	0.0989	204.1	0.8528	
Rice	*Pyricularia oryzae* (Lesion)	2nd infection	2.245	13.83	0.6624	Yanagita & Shindo, unpublished
		[c]	1.9740	9.902	0.8966	
		3rd infection	0.8211	61.29	0.7036	

[a] According to equation (4) in meter.
[b] Coefficient of determination.
[c] Calculated in removing a tailing part of dispersal distribution, because the tailing part is not differentiated from contamination of outside sources.

lesions on the plants in the row was counted at one week intervals, which approximately corresponded to the length of infection cycle or generation time. From this experiment, a dispersal gradient (α) and the degree of increase of lesions on the initial source plant after one infection cycle (γ) were calculated as 1.97 and about 4, respectively. In this trial, 1 and 4 were used for the values of α and γ, respectively.

In the Yanagita-Shindo's experiment, plants were transplanted at a rate of one plant for 23 cm. The dispersal gradients (α) in Table 1 were calculated with the meter as a unit of distance. However, it is more convenient to take the distance between plants as a unit in the simulation of the disease increase. The value of α calculated in the Yanagita-Shindo's experiment, 1.97, was replaced by 0.453 in the plant unit of distance.

In this trial, $a=1$, $\gamma=4$, and $\alpha=0.1$ were taken as a foundation, and disease increase on each plant was compared among various α values. When α's other 0.1 are used, γ is calculated for each α by the following equation

$$\gamma = \frac{4\left(1+2\sum_{d=1}^{\infty} e^{-0.1d}\right)}{1+2\sum_{d=1}^{\infty} e^{-\alpha d}} \qquad (6)$$

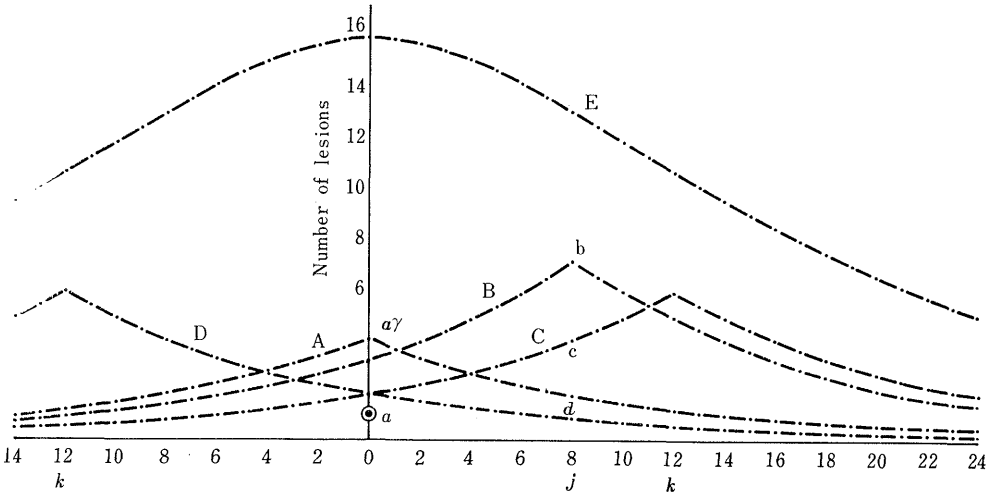

Fig. 1. A dispersal model of a pathogen with α and γ values of 0.1 and 4, respectively.
Point *a*: An initial inoculum.
Curve A: The distribution of lesions after the first infection from the initial inoculum *a*.
Curve B: The secondary dispersal distribution curve from the *j*-th plant.
Curve C: The secondary dispersal distribution curve from the *k*-th plant in the right side.
Curve D: The secondary dispersal distribution curve from the *k*-th plant in the left side.
Curve E: The total distribution curve after the second infection.
Point b: The contribution from the *j*-th plant to the increase of lesions on the *j*-th plant in the second infection.
Point c: The contribution from the *k*-th plant in the right side to the increase of lesions on the *j*-th plant in the second infection.
Point d: The contribution from the *k*-th plant in the left side to the increase of lesions on the *j*-th plant in the second infection.

based on the assumption that the infection rate is always same.

After the first infection, the number of susceptible type lesions is distributed according to equation (4). After the second infection, spores are dispersed according to the same equation, again, from each plant with susceptible lesions. After the i-th infection, the number of susceptible type lesions on the j-th plant from the initial source plant, $y_j^{(i)}$, is calculated by the following equation

$$y_j^{(i)}=\gamma\left[y_0^{(i-1)}e^{-j\alpha}+\sum_{k=1}^{\infty}y_k^{(i-1)}(e^{-|k-j|\alpha}+e^{-|k+j|\alpha})\right]. \qquad (7)$$

The j-th plant receives the effective spores of $\gamma y_0^{(i-1)}e^{-j\alpha}$ from the initial source plant, 0-th plant, those of $\gamma y_k^{(i-1)}e^{-|k-j|\alpha}$ from the k-th plant on the same side as the j-th plant and those of $\gamma y_k^{(i-1)}e^{-|k+j|\alpha}$ from the k-th plant on the opposite side in the distribution shown in Fig. 1. Thus, the total number $y^{(i)}$ of susceptible type lesions in the row of susceptible plants after the i-th infection is calculated according to

$$y^{(i)}=2\sum_{j=0}^{\infty}y_j^{(i)}-y_0^{(i)}. \qquad (8)$$

By these equations, the total number of susceptible lesions and the distribution of the lesions till the 100-th plants in each infection generation were calculated with a computer as partly shown in Table 2.

Table 2. The number of lesions in one side of disease dispersal after one to five generations in pure and mixed stands ($\alpha=0.05$)

Plant number	Pure stand					Mixed stand				
	I[a]	II	III	IV	V	I	II	III	IV	V
0	2.0	81.3	4912	3296×10^2	2319×10^4	2.0	40.7	1231	4232×10	1454×10^3
1	1.9	81.2	4910	3295	2319					
2	1.8	80.9	4903	3293	2317	1.8	40.5	1229	4128	1453
3	1.7	80.4	4893	3288	2315					
4	1.6	79.8	4879	3283	2312	1.6	40.0	1223	4115	1450
5	1.6	79.1	4861	3275	2308					
6	1.5	78.3	4839	3266	2304	1.5	39.2	1213	4096	1445
7	1.4	77.3	4814	3256	2298					
8	1.4	76.3	4785	3243	2292	1.4	38.2	1199	4066	1437
9	1.3	75.1	4752	3230	2285					
10	1.2	73.9	4716	3215	2277	1.2	37.0	1182	4030	1428
15	1.0	67.2	4494	3117	2226					
20	0.7	59.8	4214	2988	2158	0.7	29.9	1056	3746	1353
25	0.6	52.4	3897	2834	2073					
30	0.4	45.3	3559	2660	1976	0.5	22.7	891	3334	1239
35	0.4	38.8	3214	2474	1867					
40	0.3	33.0	2875	2280	1751	0.3	16.5	720	2856	1098
45	0.2	27.8	2549	2082	1630					
50	0.2	23.3	2242	1888	1505	0.2	11.7	561	2365	943
Total	80.0	6331	494300	3818×10^4	2925×10^6	40.0	1584	61840	2388×10^3	9149×10^4

[a] Infection generation.

Disease increase in the mixed stand of resistant and susceptible plants

The use of multiline variety has been supported by the development of isogenic lines which have different resistance genes from each other. In the field, spores formed on the source plants should be dispersed in the same way in the mixed stand of susceptible and resistant varieties as in the pure stand of susceptible variety, because of their isogenic nature except their disease resistance; accordingly they have same morphological characteristics.

Therefore, equation (4) can be applied also in the mixed stand with the same values of α and β as in the pure stand. The difference is only the inability to develop lesions on the resistant plants.

In the mixed stand, assume that susceptible and resistant plants are alternately planted. Equations (7) and (8) can be applied by removing odd-numbered plants. Thus, the right half of Table 2 was calculated.

Dispersal gradient

This investigation was carried out on the basis of the information on the dispersal of pathogens. It is interesting to compare the dispersal gradient obtained in the present paper with those in literature.

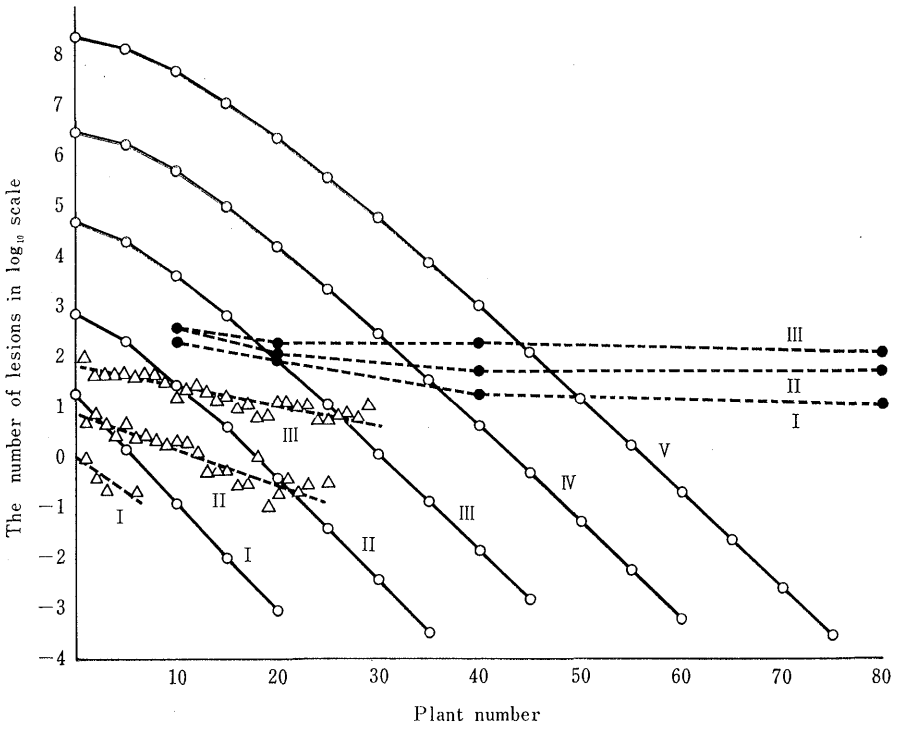

Fig. 2. The dispersal distribution curve in semi-log scale.

○——○: The distribution after the 1st to 5th infection generations of a pathogen with α of 0.5 in the plant unit.

△—·—·—△: The distribution after the 1st to 3rd generations of *Pyricularia oryzae* (Yanagita and Shindo, unpublished).

●— — —●: The distribution after the 1st to 3rd generations of *Puccinia graminis* (Cammack, 1958).

In the present simulation, the first infection from a point source shows a straight line in a semi-log scale. After the second infection, dispersal curves are parallel to the first gradient at large distances from the source, but flattened near the source (Fig. 2). Such flattening after some infection cycles has been observed, for example, by Cammack[3] and Yanagita and Shindo (unpublished) (Fig. 2). In their data, the dispersal gradients decrease with increasing infection cycles. Such a decrease of the gradient is found in the present simulation as shown in Fig. 2. There, however, is a difference in the too short distances between each of the curves as compared with the present simulation.

The distance between dispersal curves in a log scale indicates the rate of increase of lesion number on each plant. Therefore, the shorter distance between the curves near the

Table 3. Total number of lesions after various generations of infection for various dispersal gradients, and the rate of increase of lesion number between generations (in parentheses)

α	γ	Stand	Infection generation				
			I	II	III	IV	V
0.01	0.6351	Pure	0.8006×10^{2}	0.5915×10^{4}	0.4315×10^{6}	0.3142×10^{8}	0.2288×10^{10}
				(73.87)	(72.95)	(72.82)	(72.80)
		Mixed	0.3992×10^{2}	0.1470×10^{4}	0.5349×10^{5}	0.1942×10^{7}	0.7051×10^{8}
				(36.83)	(36.38)	(36.31)	(36.30)
0.02	0.9274	Pure	0.8006×10^{2}	0.9567×10^{6}	0.4334×10^{6}	0.3122×10^{8}	0.2244×10^{10}
				(74.53)	(72.64)	(72.04)	(71.86)
		Mixed	0.3997×10^{2}	0.1487×10^{4}	0.5392×10^{5}	0.1939×10^{7}	0.6957×10^{8}
				(37.20)	(36.26)	(35.96)	(35.87)
0.05	2.0151	Pure	0.8006×10^{2}	0.6332×10^{4}	0.4943×10^{6}	0.3818×10^{8}	0.2925×10^{10}
				(79.09)	(78.07)	(77.27)	(76.62)
		Mixed	0.4005×10^{2}	0.1584×10^{4}	0.6184×10^{5}	0.2388×10^{7}	0.9149×10^{8}
				(39.55)	(39.04)	(38.62)	(38.30)
0.10	4.0000	Pure	0.8006×10^{2}	0.6409×10^{4}	0.5128×10^{6}	0.4099×10^{8}	0.3274×10^{10}
				(80.05)	(80.02)	(79.95)	(79.86)
		Mixed	0.4013×10^{2}	0.1611×10^{4}	0.6457×10^{5}	0.2588×10^{7}	0.1036×10^{9}
				(40.12)	(40.10)	(40.07)	(40.03)
0.20	7.9797	Pure	0.8006×10^{2}	0.6410×10^{4}	0.5132×10^{6}	0.4109×10^{8}	0.3290×10^{10}
				(80.06)	(80.06)	(80.06)	(80.06)
		Mixed	0.4042×10^{2}	0.1635×10^{4}	0.6608×10^{5}	0.2672×10^{7}	0.1081×10^{9}
				(40.43)	(40.43)	(40.43)	(40.43)
0.50	19.6089	Pure	0.8006×10^{2}	0.6410×10^{4}	0.5132×10^{6}	0.4109×10^{8}	0.3290×10^{10}
				(80.06)	(80.06)	(80.06)	(80.06)
		Mixed	0.4243×10^{2}	0.1801×10^{4}	0.7640×10^{5}	0.3242×10^{7}	0.1376×10^{9}
				(42.43)	(42.43)	(42.43)	(42.43)
1.00	36.9984	Pure	0.8006×10^{2}	0.6410×10^{4}	0.5132×10^{6}	0.4109×10^{8}	0.3290×10^{10}
				(80.06)	(80.06)	(80.06)	(80.06)
		Mixed	0.4858×10^{2}	0.2360×10^{4}	0.1147×10^{6}	0.5570×10^{7}	0.2706×10^{9}
				(48.58)	(48.58)	(48.58)	(48.58)

source than that at large distances from the source indicates a smaller increase of lesions on plants near the source. Such an extremely small increase of lesions on plant near the source may be due to the underestimation by multiple infections in the same point or prevention of increase of lesions by a limitation of healthy tissue. Cammack[3] pointed out the contamination of spores from outside sources and increasing infection cycles as reasons for flattening of dispersal gradient. Besides, the repression of the increase of lesions by a multiple infection or a limitation of healthy area of leaves is presumed to be very important for flattening of dispersal curves.

Effect of mixture of resistant plant

In order to know the effect of mixture of resistant plants, the number of lesions in both stands (Table 3) and its ratio of the mixed stand to the pure stand for each α value (Table 4) were calculated. The ratio decreases as the generation increases.

Leonard (1969a) stated that the relative amounts of rust in the two fields, the pure and mixed stands, are given by

$$\frac{y'}{y_0}=m^n\frac{y}{y_0}, \qquad (9)$$

where y_0 is the proportion of host tissue initially infected, y' is the proportion of infected host tissue in mixed stand, m is the proportion of susceptible plants in the host mixture, and n is the number of generations of rust increase. This equation can strictly be applied only when the epiphytotic starts from a single pustule or lesion in each field, and after n generations, there will be approximately equal numbers of pustules in both fields, but if the distribution of the pathogen is random, half of the pustules in mixed stand will be on resistant plants. If the value of α in equation (4) is close to 0, this condition is satisfied.

In the uppermost line of Table 3, ratios calculated by equation (9) are shown. For $\alpha=$ 0.01-0.20, the ratios of mixed stand to pure stand agree with the ratio calculated by equation (9). The ratios increase as the value of α increases for α values over 0.20. This indicates that equation (9) cannot be applied when α is over 0.20. Under such a condition, the distribution of spores is not random on susceptible and resistant plants. This is due to that spores released from the lesions are ununiformly dispersed, mainly on the source plants, and decreasingly on

Table 4. The ratio of the number of lesions in mixed stand to that in pure stand

α	Infection generation				
	I	II	III	IV	V
Random[a]	0.50	0.25	0.13	0.06	0.03
0.01	0.50	0.25	0.12	0.05	0.03
0.02	0.50	0.25	0.12	0.05	0.03
0.05	0.50	0.25	0.12	0.06	0.03
0.10	0.50	0.25	0.13	0.06	0.03
0.20	0.50	0.26	0.13	0.07	0.03
0.50	0.53	0.28	0.15	0.08	0.04
1.00	0.61	0.37	0.22	0.14	0.08

[a] Values calculated by equation (9).

the surrounding plants. This, furthermore, indicates that the effect of mixture of resistant plants to inhibit the increase of the pathogen decreases as the values of α increase. Its critical value is between 0.2 and 0.5 of the values calculated in the plant unit. In Table 1, the values of α calculated in meter unit are shown. When the product of the α value in Table 1 and the distance between plants in meter is smaller than 0.2, equation (9) can be applied.

Mathematical notes

Let us consider mathematically the increase of the total numbers of lesions in one row in infinite length in which two varieties with different susceptibility are alternately grown and a central plant has a susceptible type lesions and other plants have no lesions. Assume that lesion number increases for each generation by the rates of γ_e and γ_o on the even-numbered and odd-numbered plants from the central inoculum plant, respectively, by spores produced on its own plants, namely without counting lesions formed by spores dispersed from other plants, and the number of lesions on the j-th plants after the first generation, $y_j^{(1)}$, is expressed by the following equations ($j=0,1,2,\cdots$).

$y_j^{(1)}=a\gamma_e e^{-|j|\alpha}$ when j is even

and

$y_j^{(1)}=a\gamma_o e^{-|j|\alpha}$ when j is odd,

where α denotes dispersal gradient of lesions and the figures in parentheses represent the generation. Accordingly, the total number of lesions on even-numbered plants ($T_e^{(1)}$) and that on the odd-numbered plants ($T_o^{(1)}$) after the first generation are represented as

$$T_e^{(1)}=\sum y_{2n}^{(1)}=a\gamma_e\sum e^{-|2n|\alpha}=a\gamma_e\frac{1+e^{-2\alpha}}{1-e^{-2\alpha}} \tag{10}$$

and

$$T_o^{(1)}=\sum y_{2n-1}^{(1)}=a\gamma_o\sum e^{-|2n-1|\alpha}=a\gamma_o\frac{2e^{-\alpha}}{1-e^{-2\alpha}}, \tag{11}$$

where $n=\cdots,-2,-1,0,1,2,\cdots$. Putting $\frac{1+e^{-2\alpha}}{1-e^{-2\alpha}}=p$ and $\frac{2e^{-\alpha}}{1-e^{-2\alpha}}=q$, equations (10) and (11) are reduced to the following two equations.

$T_e^{(1)}=a\gamma_e p$

and

$T_o^{(1)}=a\gamma_o q$.

The total number of lesions in the row is given by

$T^{(1)}=T_e^{(1)}+T_o^{(1)}=a(\gamma_e p+\gamma_o q)$.

After the u-th generation, the total number of lesions on the even-numbered plants and that on the odd-numbered plants are represented as the difference equations

$T_e^{(u)}=\gamma_e pT_e^{(u-1)}+\gamma_e qT_o^{(u-1)}$ for the even-numbered plants (12)

and

$T_o^{(u)}=\gamma_o qT_e^{(u-1)}+\gamma_o pT_o^{(u-1)}$ for the odd-numbered plants, (13)

where $u=0,1,2,\cdots$, and the first and second terms of the right side in both equations are the contributions from the even- and odd-numbered plants, respectively. The following solution can be obtained from equations (12) and (13).

$$T_e^{(u)}=a\gamma_e p\frac{\rho_1^u-\rho_2^u}{\rho_1-\rho_2}-a\rho_1\rho_2\frac{\rho_1^{u-1}-\rho_2^{u-1}}{\rho_1-\rho_2} \tag{14}$$

and

$$T_o^{(u)}=a\gamma_o q\frac{\rho_1^u-\rho_2^u}{\rho_1-\rho_2}, \tag{15}$$

where ρ_1 and ρ_2 are the roots of $\rho^2-(\gamma_e p+\gamma_o p)\rho+\gamma_e\gamma_o p^2-\gamma_e\gamma_o q^2=0$. The total number of lesions after the generation is

$$T^{(u)}=T_e^{(u)}+T_o^{(u)}=a(\gamma_e p+\gamma_o q)\frac{\rho_1{}^u-\rho^u{}_2}{\rho_1-\rho_2}-a\rho_1\rho_2\frac{\rho_1{}^{u-1}-\rho_2{}^{u-1}}{\rho_1-\rho_2}. \quad (16)$$

From this equation, we can get the total number of lesions at any generation for any values of γ_e and γ_o.

For example for $u=2$, we can easily get the following results from equations (14) and (15).

$$T_e^{(2)}=a\gamma_e p(\rho_1+\rho_2)-a\rho_1\rho_2$$
$$=a\gamma_e p(\gamma_e p+\gamma_o p)-a(\gamma_e\gamma_o p^2-\gamma_e\gamma_o q^2)$$
$$=a(\gamma_e{}^2p^2+\gamma_e\gamma_o q^2) \quad \text{and so on.}$$

The following results in special cases are obtained under some conditions.

(1) If the rate of increase of lesions on a plant by spores dispersed from lesions on its own plant is equal in all the plants, *i.e.*, $\gamma_e=\gamma_o$,

$$T^{(u)}=a\gamma_e{}^u(p+q), \quad (17)$$

where

$$p+q=\frac{1+e^{-\alpha}}{1-e^{-\alpha}}.$$

(2) If the rate of increase of lesions on odd-numbered plants by spores dispersed from the lesions on their own plants is zero, *i.e.*, $\gamma_o=0$,

$$T^{(u)}=a(\gamma_e p)^u \quad (18)$$

Values calculated by equations (17) and (18) for pure stand of susceptible plants and mixed stand of resistant and susceptible plants in an equal proportion agreed with the values shown in the last row in Table 2. However, we cannot estimate the number of lesions on each plant, because its estimation by mathematical method is very onerous.

Acknowledgements

The authors are indebted to Mr. Hiroshi Fujimaki, Dr. Tadakazu Okuno and Mr. Shiro Okabe for their valuable suggestions.

The computation of the exact values in Tables 2 and 3 was made based on the program written by Mr. Hiroshi Fujimaki in the Computing Center for Research in Agriculture, Forestry and Fishery. Assistance of the computing center is also acknowledged.

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和文摘要

病害防除のための抵抗性品種混合の効果に関する理論的研究

清沢茂久・塩見正衛

病害防除のための多系混合方式の効果を知るために，罹病性品種の単独栽培と抵抗性品種と罹病性品種の混合栽培における病勢進展の比較に関する模擬試験を電子計算機を利用して行なった。

種々の病原菌の飛散胞子の分布は $y=\beta e^{-\alpha d}$ に従う（y は病斑数あるいは胞子数，d はメートル単位の距離，α と β はそれぞれ飛散勾配と伝染源植物上の病斑数）。

もし株間距離を距離の1単位としてとったときの α の値が 0.2 以下であるならば，罹病性植物集団の中に 1：1 の割合で抵抗性植物を混合したことによる病勢進展の抑制は Leonard の $(y'/y_0)=m^n(y/y_0)$ $(y, y'$ はそれぞれ単独栽培と混合栽培における n 伝染世代後の病斑数，y_0 は伝染開始期の病斑数，m は罹病性植物の混合比率）で表わされる。抵抗性品種混合の効果は α が 0.2 以上になると上式で示されるよりもその効果は小さくなる。

実際の圃場では，重複感染が Cammack が指摘した外部からの胞子の混入や伝染世代の増加と同様に飛散胞子分布曲線の平担化に重要な役割を果しているものと考えられた。