Effect of Addition of Field Resistance to Variety with True Resistance

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Synopsis. It has a deep significance in breeding to predict the utility value of a variety which will be developed in the future. In the present paper, stability or longevity of a variety with both field and true resistances is estimated on the basis of models that were given up to now for daily increase of disease.

Introduction

It is sometimes reported that resistant varieties developed for high degree of disease resistance are severely attacked by newly developed races. Such a breakdown of resistance compels a change in the program of breeding for disease resistance.

In the past, field resistance has been used in breeding for disease resistance followed by true resistance in most of the cases where resistance could be divided into two groups, true and field.

After the defect of use of true resistance alone was realized, the following new methods for controlling disease by breeding have been proposed: (1) addition of field resistance to true resistance, (2) accumulation of true resistance genes (Kiyosawa, 1965) and (3) multiline variety (Jensen, 1952, Borlaug, 1959).

It is not yet established how to determine the best method. Comparison of these methods by developing varieties with various resistances and growing them in farms is very difficult and requires a long time. It is therefore necessary to find a way for comparing these methods theoretically and experimentally.

Kiyosawa (1972b) devised a way for studying theoretically the utility value of a multiline variety (mixture cultivation of lines with different genotypes) in comparison with the rotational cultivation of these lines which has usually been employed regardless of our like or dislike when a resistant variety is breakdown.

The present work is aimed to know the effect of addition of field resistance to true resistance.

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Expression of True Resistance and Field Resistance in Daily Disease Increase

Reduction of horizontal (non-specific) resistance by introducing vertical resistance is known as Vertifolia effect in relation with the breakdown of the potato variety Vertifolia (van der Plank, 1963). The loss of non-specific resistance during a process of breeding for specific resistance and/or a pleiotropic function of specific resistance gene to reduce non-specific (or field) resistance are considered as the cause of the Vertifolia effect. There is no evidence however to show which is the correct one except some reports (Asaga and Yoshimura, 1969, 1970, Ezuka, et al., 1970, Hirano, et al., 1966, 1971, Suzuki and Iwano, 1963) supporting the former hypothesis.

The present work was done from the standpoint of the former hypothesis.

Van der Plank (1963) divided disease resistance into two groups, vertical resistance and horizontal resistance, and stated that both resistances are expressed by and in the equation

\[ x = x_0 e^{rt}, \]

where \( x \) and \( x_0 \) are the proportion of diseased tissue at time \( t \) and 0, respectively, and \( r \) is the infection rate in disease within a year (daily increase).

On the other hand, Kiyosawa (1965) proposed the equations

\[ y = y_0 e^{rt} \]

and

\[ y = \frac{Y}{1 + ke^{-rt}} \]

(3)

as models for disease increase. Here, \( y \) and \( y_0 \) are the number of lesions at the time \( t \) and 0, and \( Y \) is the upper limit or final value.
of the number of lesions. Equations (2) and (3) were obtained by integrating the equations
\[ \frac{dy}{dt} = ry \quad (4) \]
and \[ \frac{dy}{dt} = ry(1 - \frac{y}{Y}) \quad (5) \]
respectively. Equation (2) has a wider range of application than equation (1) (Kiyosawa, 1968). In equations (2) and (3), true resistance and field resistance are defined to be the resistance influencing \( y_0 \) and \( r \), respectively (Kiyosawa, 1970).

**Yearly Fluctuation of Disease Severity**

There are very few available data in Japan on yearly changes of the disease severity or yield loss due to disease. Regressions of cumulative spore numbers and yield loss due to blast disease on year were examined on the data collected in Nagano Prefecture (Kuribayashi and Ichikawa, 1952) (Fig. 1), and described in Crop Statistics. In both cases, a significance was not obtained in the regression, although large fluctuations were observed in these quanta. This indicates that there is no tendency toward increase or decrease of disease severity in the past. Furthermore, this indicates that disease severity is almost same in every year if there is no yearly fluctuation of environmental conditions, namely under the standard conditions defined by Kiyosawa (1965).

There are many reports in which virulent races increased gradually after release of a new resistant variety (Fleischmann, et al., 1963, Green, 1971, Green, et al., 1961, Johnson, 1956, Loebering, 1949, Simons and Michel, 1961, Watson and Luig, 1963). It is expected that the increase of virulent races is more smooth under the standard conditions than under natural conditions. Such an increase curve may show a plateau over the level of old variety when the Vertifolia effect appears. When the lesion numbers at the time 0, initial time of infection, in each year are connected, we could expect the figure as shown in Fig. 2. In this figure, the upper curves are for a variety with only field resistance and lower curves are for a variety with true resistance and without field resistance. Which curve can we obtain when the field resistance expressed by the upper curves is added to the true resistance expressed by the lower curves? Is it curve A, B or C in the figure? The present study

![Figure 1](image1.png)

*Fig. 1. The final cumulative spore numbers during 12 years and its regression line.*

![Figure 2](image2.png)

*Fig. 2. Daily and yearly curves of disease increase of an old variety with true resistance.*
was conducted to determine this point. If we can get curve C in complete combination of true and field resistance in Fig. 2, the newly obtained variety may not break down permanently. It is very important to know the degree to which the field resistance contributes to stability of true resistance in the newly obtained variety.

Models for Daily Disease Increase

The words, field resistance and true resistance, were defined in relation to the nature of daily increase of disease (Kiyosawa, 1970). However, the utility value of a newly developed variety is generally related to yearly increase of disease. Accordingly, we must get the relation between daily curve and yearly curve of disease increase after making clear the nature of daily increase.

As models for daily increase of disease, the equations were used

\[ y = y_0 e^{r(1 - e^{-\frac{t}{T}})} \]  
\[ y = \frac{Y'}{1 + ke^{-r(1 - e^{-\frac{t}{T}})}} \] (7)

by Kiyosawa (1968), and

\[ y = \frac{Y'}{1 + ke^{-\frac{t}{T}}} \]
\[ k = \frac{Y' - y_0}{y_0} \] (8)

by Burleigh, et al. (1969). These equations were obtained by integrating the equations

\[ \frac{dy}{dt} = ry(1 - \frac{t}{T}) \] (9)
\[ \frac{dy}{dt} = ry(1 - \frac{y}{Y'})(1 - \frac{t}{T}) \] (10)
and

\[ \frac{dy}{dt} = ry(1 - \frac{y}{Y'}) \] (11)

respectively. Here, \( T \) is the terminal time of infection and \( Y' \) is the maximum of final lesion numbers during past some years.

Kiyosawa (1972a) calculated infection rate \( r \) and lesion number at the initial time of infection \( y_0 \) in each year using equations (3), (6) and (8). From this data, the average of infection rates is obtained as follows.

Equation

\[ r \]
\[ 0.149 \]
\[ 0.193 \]
\[ 0.079 \]

At first, let us consider yearly curve when field resistance is combined with true resistance in the case where equation (6) is used. In Fig. 3, the value of \( y_0 \) is given a priori as 0.1 at the first year, and the value of lesion number at \( t = T = 95 \) which is the duration of infection under the average conditions in test place in Nagano Prefecture is calculated by using equation (6) with average infection rate shown above. Furthermore, overwintering rate \( \theta \) was calculated by \( y_0 \) and \( y_T \) to get a yearly curve parallel to abscissa. This curve corresponds to the yearly curve of old variety with field resistance. When the resistance decreasing the amount of virulent races by 1/100 is added to the old variety, yearly curve of disease increase on the new variety may start at 0.001 of lesion (cumulative spore) number. The value of lesion number at the terminal time \( (y_T) \) at the first year, \( y_{T,0} \), was calculated using equation (6) by giving the same value of infection rate as used for the old variety. Then, the yearly curve for the new variety is obtained by giving the same value of \( \theta \) as used for the old variety, as shown in Fig. 3. In this case, the obtained yearly curve of disease increase is parallel to abscissa. When slightly high \( r \) or \( \theta \) value was given in the calculation of Fig. 3, curves in Fig. 4 were obtained for varieties with various true resistance scores. In this case, it is noticed that all yearly curves are parallel to each other. This agrees with
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Fig. 4. Yearly increase of disease on varieties with various true resistance when the equation \( y = y_0 \exp \left( \frac{t - T}{2T} \right) \) is used.

Fig. 5. Yearly increase of disease on a variety with true resistance when the equation \( y = Y'_{\lambda} \left( 1 + ke^{-\frac{r}{2T}} \right) \) is used.

The results obtained previously by Kiyosawa (1972b) in which the equation
\[
\frac{T}{2} r + \log_e \theta = \lambda \tag{12}
\]
was obtained as the relation between infection rate \( r \) and fitness of pathogen (yearly infection rate, \( \lambda \)), when equation (6) is applied. Such yearly curves as shown in Figs. 3 and 4 are probably expected only in unlimited amounts of host plants.

In the same way, Fig. 5 is obtained when equation (8) is used. In this case, the yearly curve reaches a plateau within a year, showing that true resistance has little effect on control of disease. This calculation is not true at least in the case of breakthrough of the rice variety Kusabue which was severely attacked 3 years after its release (Yamada, 1965, Ito, 1967).

Both calculations do not agree with practical phenomena. This is probably due to disregard of density effect in equation (6) and to disregard of environmental suppression against disease increase in equation (8).

Equation (6) contains an increasing inhibition of disease increase with the progress of time, perhaps by the increase of resistance due to the change of plant age and environmental conditions, and equation (8) includes a limitation of the amount of host plants, as shown by \( \left( 1 - \frac{t}{T} \right) \) and \( \left( 1 - \frac{Y'}{Y^*} \right) \) in equations (9) and (11), respectively. These two factors may function in practical disease increase. Therefore, equation (7) which is obtained by combining both factors was used. The result is shown in Fig. 6. In the same way, various yearly curves were drawn for various \( y_0 \) values (Fig. 7). These curves are likely to fit practical phenomena better than the above two numerical calculations.
the best and equation (6) was the second for fitting the data. On the other hand, Chiba, et al. (1972) compared equations (3) and (6) with better fitness in the latter. However, a good fitness does not always indicate that the equation can adequately express the nature of daily increase. We must develop a better mathematical model for such an investigation. Such a work must be separately carried out in various regions, for the property of daily increase of disease is different from region to region.

Generally speaking, more practical prediction on the longevity or stability of resistant variety could be obtained by more correctly expressing in the equation the property of daily disease increase for propagation of pathogens on the host plant. This must be done by getting more delicate field data.

To know the density effect on propagation of pathogen in the field is one of the most important problems. Leonard (1969) demonstrated experimentally the presence of negative density effect by examining the relation between sporulation and the number of pustules on a leaf. Chiba, et al. (1972) found a negative regression \( r = -0.039 \log e y_t + 0.437 \) of infection rate against logarithmic number of lesions at the first recording time (\( \log e y_t \)) under some field conditions in Aomori Prefecture. A yearly curve by giving the correction factor \( r' = r - 0.039 \log e y_t \) for \( r, T=50 \) and \( r=0.36 \) in equation (6) was calculated by the author. In this case, \( T=50 \) is the duration of infection under the field conditions in Aomori Prefecture, and \( r=0.36 \) is the average of infection rates. The result of calculation showed a severe increase of disease, indicating that such a correction of \( r \) is not suitable for estimation of yearly increase. It may be
reasonable for density effect on disease increase may increase gradually but not constant through the process of disease increase. The general application of the correction of \( r \) value by \text{Chiba, et al.} (1972) appears questionable.

Accuracy of calculation is dependent upon whether the model for daily increase of disease is suitable for each region. Models for daily increase are not still sufficient. Therefore, we must endeavor to express the property of daily increase of disease in a mathematical model. The prediction of stability and longevity of a resistant variety, and comparison of methods for controlling disease epidemics by breeding may become possible through such theoretical and experimental studies.

**Summary**

Using three models for increase of disease within a year (daily increase), (a) \( y = y^* e^{r (t - \frac{t_1}{2})} \), (b) \( y = \frac{Y^*}{1 + ke^{-r t}} \) and (c) \( y = \frac{Y^*}{1 + k e^{-r (t - \frac{t_1}{2})}} \), the stability or longevity of a variety with a combination of true resistance and field resistance was calculated. Under conditions where equation (a) is applied, newly developed resistant variety shows the largest stability among conditions expressed by the three equations. However, equation (c) seems to be most practical, for the obtained yearly increase of disease is similar to practical increase of disease.

Yearly curve of disease increase, accordingly longevity or stability of a resistant variety, is profoundly influenced by the nature of daily increase of disease. Therefore, model for daily increase of disease that is able to express faithfully the nature of a daily increase must be developed on the basis of many data which must be observed in field and laboratory.

**Literature Cited**


真性抵抗性をもつ品種への圃場抵抗性付加の効果

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高度抵抗性を導入した品種の罹病化の後に、新しい育種の方法がいくつか提案されている。しかし、それらの方法の中どれが最も適した方法であるかを知るための適当な方法がないのが現状である。

ここでは、圃場抵抗性をもつ品種にその圃場抵抗性を落さずに真性抵抗性を入れた場合、えられた品種が、環境条件の年次変動のない標準条件の下で、どのような抵抗性を示すかを、これまでに提出されている病原菌の年の増殖モデルと観察を組み合わせて数値計算を行なった。

年内的増殖曲線が \( y = \frac{\ln b}{1+ke^{-rt}} \) で示されるような条件の下では、永久に罹病化しない品種がえられる。しかし、この式は圃場抵抗性をわずかに落したような場合に適用できるかどうかに疑問がもたれる。

S字型を示す年内的増殖曲線に式 \( y = \frac{\ln b}{1+ke^{-(r-\frac{1}{2})t}} \) が適用できるような条件では、真性抵抗性の利用価値はほとんどない。しかし、このような条件も実際には存在しうる可能性はきわめて少ない。

両式を組み合わせた \( y = \frac{\ln b}{1+ke^{-\left(1+\frac{1}{2}\right)t}} \) を用いると、導入された真性抵抗性により、そのレベルが異なる年間増殖曲線をえた。初め平行に上昇し、後に在来品種の示す水平な年間増殖曲線に漸近する。この数式が現在知られている限りでは最も実際に近いものと考えられる。


