

A MATHEMATICAL APPROACH TO THE PREDICTION OF DIFFERENCES IN THE RELATIVE ABILITY OF RACES OF *PUCCINIA GRAMINIS TRITICI* TO SURVIVE WHEN MIXED

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Abstract

A model describing the population trends for any number of races of rust in the urediospore stage during a single growing season is presented. The general case for the field is subsequently modified to describe trends in a population of rust races under constant conditions. A term which gives an estimate of the relative survival ability of each race in the population is finally obtained. This term allows the trends in the composition of the mixture to be predicted. The theoretical proportion of strain 21 Anz-2,3,7 in a mixture of strains 21 Anz-2,7 and 21 Anz-2,3,7 of *P. graminis tritici* over a number of generations was compared with the proportion of strain 21 Anz-2,3,7 in an experimental population of the same two strains over the same period. The model was found to be a good first approximation to the results obtained with the experimental population.

I. INTRODUCTION

Changes in the incidence of physiologic races or strains of cereal rusts in the field are well known (Stakman and Christensen 1960). Many changes occur as a direct result of the replacement of existing host varieties by varieties possessing different factors for resistance (Person 1967), but fluctuations in the incidence of rust races in the absence of variety changes have also been reported (Kak *et al.* 1963; Prasada *et al.* 1966; Katsuya and Green 1967). Such changes have been attributed to many factors, including the differing ability of rust races to survive in association with each other (Watson 1958).

Katsuya and Green (1967) cited the example of strains 15B-3 and 15B-5 of *Puccinia graminis* Pers. f. sp. *tritici* Eriks. & Henn. which appeared in Canada several years earlier. Although these races were virulent on the predominantly grown wheat variety Selkirk, their survival ability relative to the field rust population at the time was apparently low and they soon disappeared. If the early disappearance of races such as 15B-3 and 15B-5, which threaten the principally grown wheat varieties, could be predicted, much concern and plant breeding effort could be saved. The value of methods for predicting the behaviour of races or strains of the pathogen present in the field is obvious.

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Watson (1942) found that it was impossible to predict differences in the relative ability of rust races to survive when mixed by comparing the behaviour of the component races when grown singly. However, Bromfield and Broyles (1952) and Broyles (1955) reported that the difference in survival ability between any two races could be predicted from their behaviour in a mixture with a common standard race. To the best of our knowledge, a mathematical treatment of population trends in a mixture of races of plant pathogenic fungi has not been previously attempted. The following model is similar to earlier models (Landahl 1955; Taylor 1968) describing competition in populations of the flour beetle, *Tribolium* sp.

II. DESCRIPTION OF THE MODEL

The model as given is suitable for a systems analysis approach. Although only a simplified form is required in the present paper, it could be generalized and adjusted without difficulty to take more detailed data into account, and could easily be programmed for a computer. Furthermore, the model as given in the paper is flexible. If there were some interaction between species, terms to describe this could easily be introduced, and changes in any of the parameters from generation to generation could also be included.

Suppose there are n races in a population and let a given race be denoted by the subscript i . Let

$N_i(t)$ = the number of uredia of race i at time t ,

$\Delta N_i(\tau, t)$ = the number of uredia aged between $\tau - \Delta t$ and τ at time t ,

$\pi_i(\tau, t)$ = the probability of survival for time Δt of a uredium of age τ at time t ,

a_i = the average life span of uredia of race i ,

r_i = the proportion of infection courts of race i that develop into uredia on a given host,

$\sigma_i(\tau, t)$ = the average size of a uredium of age τ at time t ,

$s_i = \sigma_i(a_i, t)$, the size of a uredium developed in time a_i under the given conditions,

$k_i = \Delta \sigma_i / \Delta t$, the rate of growth of a uredium,

β_i = the number of urediospores per unit size in a fully developed uredium,

q_i = the proportion of urediospores which germinate.

In general, the parameters $\pi_i, \dots, q_i$ will depend on the environment and, in some cases, also on the populations themselves.

Since $\pi_i(\tau, t)$ is the proportion of uredia of race i of age τ which survive for a time Δt , we have

$$\Delta N_i(\tau + \Delta t, t + \Delta t) = \pi_i(\tau, t) \cdot \Delta N_i(\tau, t), \quad (1)$$

for $\tau = \Delta t$ to $a_i - \Delta t$, and $i = 1, 2, \dots, n$. The number of newly formed uredia in the next generation is given by

$$\Delta N_i(\Delta t, t + \Delta t) = r_i q_i \beta_i \sigma_i(a_i, t) \cdot \Delta N_i(a_i, t), \quad (2)$$

for $i = 1, 2, \dots, n$.

As well as equations to describe the number of uredia in each generation (1), and the number of uredia in the subsequent generation in relation to the number in the previous generation (2), a second set of equations is needed to describe the growth of uredia and to determine the size (s_i) of uredia developed in time a_i under the given conditions.

Since the growth of uredia in time Δt is $\Delta\sigma_i = k_i\Delta t$,

$$\sigma_i(\tau + \Delta t, t + \Delta t) = \sigma_i(\tau, t) + k_i\Delta t, \quad (3)$$

for $\tau = \Delta t$ to $a_i - \Delta t$, and $i = 1, 2, \dots, n$. Since the size of uredia developed is initially zero,

$$\sigma_i(\Delta t, t + \Delta t) = 0, \quad (4)$$

for $i = 1, 2, \dots, n$.

The equations (1), (2), (3), and (4) give the number and sizes of uredia of each age range of each race at time $t + \Delta t$ in terms of the number at time t , and so the history of the populations can be traced. If the functional forms of the parameters could be determined from separate experiments, the model would predict the future behaviour of strains or races in the rust population.

The total number of uredia of each race is

$$N_i(t + \Delta t) = \sum_{\tau=0}^{a_i - \Delta t} \Delta N_i(\tau + \Delta t, t + \Delta t), \quad (5)$$

for $i = 1, 2, \dots, n$.

In some particular cases the solution is simple. For successful strains on a given host a uredium, once established, is almost certain to survive for the whole time a_i . This implies the equation

$$\Delta N_i(a_i, t + a_i - \Delta t) = \Delta N_i(\Delta t, t), \quad (6)$$

which also follows from (1) when $\pi_i(\tau, t) = 1$. The right-hand side of this is given by the expression (2) with $t + \Delta t$ replaced by t . Hence

$$\Delta N_i(a_i, t + a_i - \Delta t) = r_i q_i \beta_i s_i \Delta N_i(a_i, t - \Delta t). \quad (7)$$

This gives the number of uredia about to erupt in terms of the number which erupted in the previous urediospore generation. The number of uredia increases by the factor $r_i q_i \beta_i s_i$ in each generation.

Special Case

The artificial conditions within a controlled-environment cabinet eliminate some of the environmental variables operative in the field and allow a measure of the relative survival ability of each race to be obtained. When environmental conditions remain unchanged, the factor $r_i q_i \beta_i s_i$ should remain constant and the number of uredia in any age range will increase by this factor from one generation to the next. That is, the total number of uredia of race i will increase by the factor $r_i q_i \beta_i s_i$ in time a_i .

In unit time there are $1/a_i$ intervals of length a_i , in each of which the population becomes multiplied by $r_i q_i \beta_i s_i$. Hence, we can define a quantity

$$A_i = (r_i q_i \beta_i s_i)^{1/a_i}, \quad (8)$$

for $i = 1, 2, \dots, n$, which measures the rate of increase of race i per unit time. This could be regarded as a measure of the relative survival ability of race i .

The A_i will be constant only as long as conditions remain constant. In general, they will vary with time. For example, conditions might change in such a way during a season that A_1 is greater than A_2 initially but later becomes less.

In the experimental population, in which the uredia in a given population are all the same age, the above theory holds, but could be simplified for this special case. The important quantity for a given race is A_i . A comparison of the A_i for various races under given conditions would determine which race is likely to become predominant in a mixture of the races.

For races in which the a_i (that is, the period between successive inoculations) are the same, a simpler measure of relative survival ability is

$$(A_i)^{a_i} = r_i q_i \beta_i s_i = B_i, \text{ say.} \quad (9)$$

From equation (7), the number of uredia about to erupt in terms of the number which erupted in the previous generation is given by

$$\Delta N_i(a_i, t+a_i) = B_i \Delta N_i(a_i, t),$$

where, for convenience, $t - \Delta t$ is replaced by t . The number of uredia erupting in the next generation, if conditions are kept constant, is

$$\begin{aligned} \Delta N_i(a_i, t+2a_i) &= B_i \Delta N_i(a_i, t+a_i) \\ &= (B_i)^2 \Delta N_i(a_i, t), \end{aligned}$$

and so on. Hence, the number of uredia in the m th generation is

$$\Delta N_i(a_i, t+ma_i) = (B_i)^m \Delta N_i(a_i, t). \quad (10)$$

For two races ($i = 1, 2$) in which the number of urediospores is initially the same, and the generations are of the same length, the proportion (P) of uredia of race 1 after a time corresponding to m generations is, from (10),

$$P_1 = (B_1)^m / [(B_1)^m + (B_2)^m]. \quad (11)$$

Similarly, for race 2,

$$P_2 = (B_2)^m / [(B_1)^m + (B_2)^m]. \quad (12)$$

If r_i is changed from generation to generation, it is convenient to take

$$c_i = q_i \beta_i s_i \quad (13)$$

and to write $r_{i,m}$ as the value of r_i at the m th generation. Then (10) is replaced by

$$\Delta N_i(a_i, t+ma_i) = r_{i,1} r_{i,2} \dots r_{i,m} (c_i)^m \Delta N_i(a_i, t).$$

In the case of the two races with equal length of generation, if the proportions $r_{1,m}$ and $r_{2,m}$ are the same for a given generation (even though they may vary from

generation to generation), that is, if $r_{1,m} = r_{2,m}$ for each m , then (11) is replaced by

$$P_1 = (c_1)^m / [(c_1)^m + (c_2)^m], \quad (14)$$

and (12) by

$$P_2 = (c_2)^m / [(c_1)^m + (c_2)^m]. \quad (15)$$

III. COMPARISON OF THE EXPERIMENTAL AND THEORETICAL POPULATIONS

The experimental population, commencing with a mixture of equal proportions of strain 21 Anz-2,7* and 21 Anz-2,3,7 of *P. graminis tritici*, was cultured for a number of generations of 10, 14, or 18 days duration on seedlings of the wheat variety Yalta which is susceptible to both strains. The proportion of strain 21-2,3,7 in the mixture in each generation was determined by counting the number of uredia of each strain on the differential variety W2402.† These experiments have previously been described by Ogle and Brown (1970).

TABLE 1
CALCULATION OF B_i FOR STRAINS 21-2,7 AND 21-2,3,7 OF *PUCCINIA GRAMINIS*
TRITICI ON SEEDLINGS OF THE WHEAT VARIETY YALTA

Parameter	Generation length	Strain 21-2,7	Strain 21-2,3,7
Percentage germination ($q_i \times 100$)	—	33.0	41.1
Percentage of infection courts developing into uredia ($r_i \times 100$)	—	94.4	94.2
Area (mm ²) of uredia (s_i)	10	1.71	1.89
	14	3.52	4.89
	18	3.92	7.01
Average number of urediospores per square millimetre of uredium (β_i)	10	4,000	5,800
	14	3,000	4,400
	18	4,100	5,700
$B_i = r_i q_i \beta_i s_i$ (correct to 4 significant figures)	10	2,137	4,193
	14	3,361	8,236
	18	5,014	15,260

Temperature and light were kept constant during the experiment so that the theoretical proportion of each strain in the mixture is given by equation (11) or equation (12). A number of experiments were made to determine the values of the individual parameters required for the calculation of B_i . These experiments were described by Ogle and Brown (1971). The appropriate data and the calculated values of B_i are given in Table 1. Now that the values of B_i are known for each race, they can be substituted into equation (12) to give the theoretical proportion of strain 21-2,3,7 in the mixture in each generation (race 1 = strain 21-2,7; race 2 = strain 21-2,3,7).

* Anz refers to the geographic area Australia and New Zealand.

† University of Sydney varietal accession number.

The proportions of uredia of strain 21-2,3,7 in the experimental population and in the theoretical population over a number of generations are compared in Figure 1. To test the goodness of fit of the theoretical values, a χ^2 test at the 5% level was carried out. The individual χ^2_1 values for each pair of corresponding points were added together to give a χ^2_6 when inoculations were made at 10-day intervals and a χ^2_4 when inoculations were made at 14- or 18-day intervals. Although one pair of values for each generation length differed significantly, the overall χ^2 value for each generation length was not significant.

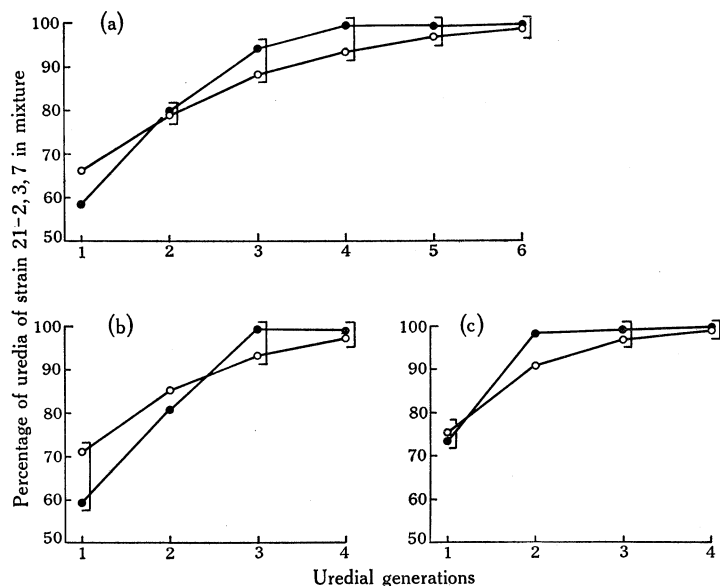


Fig. 1.—Comparison of the percentage of uredia of strain 21-2,3,7 in a mixture of strains 21-2,7 and 21-2,3,7, of *Puccinia graminis tritici* in successive generations of 10 (a), 14 (b), or 18 days (c) duration in a theoretical and an experimental population. The points linked by a square bracket did not differ significantly in a χ^2 test at the 5% level. ● Experimental population. ○ Theoretical population.

IV. DISCUSSION

A mathematical model which makes it possible to predict differences in the relative ability of races or strains of *P. graminis tritici* to survive when mixed has been presented. With the aid of the model, the proportion of each race or strain in a mixture over a number of generations can be predicted, once the factors contributing to relative survival ability have been quantitatively defined. Statistical analysis showed that the values generated by the model are a good first approximation to the results obtained experimentally. Some of the deviations from the expected results may have been due to fluctuations in environmental factors other than those controlled by the growth cabinet.

The model can be refined as more accurate knowledge of the various factors involved in determining relative survival ability becomes available. The factors that are important may vary with different combinations of races or strains of the pathogen

and the model can be altered to take these factors into account. Although the experiments were made with seedlings, the model is equally applicable to studies of rust development on more mature plants in the field. It is possible that the factors affecting relative survival ability may change as the host matures and the model may need to be adjusted accordingly.

If the necessary values could be obtained, the model could possibly be used to predict future patterns of race composition in the field rust population and therefore help to guide the direction of breeding programmes.

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VI. REFERENCES

- BROMFIELD, K. R., and BROYLES, J. W. (1952).—Marker races useful in studying survival ability of races of *Puccinia graminis tritici*. *Phytopathology* **42**, 479. (Abstr.)
- BROYLES, J. W. (1955).—Comparative studies of races and biotypes of *Puccinia graminis*, with special reference to morphology of urediospore germination, chemical composition, and factors affecting survival. Ph.D. Thesis, University of Minnesota.
- KAK, D., JOSHI, L. M., PRASADA, R. and VASUDEVA, R. S. (1963).—Survival of races of *Puccinia graminis tritici* (Pers.) Eriks. & J. Henn. *Indian Phytopath.* **16**, 117–27.
- KATSUYA, K., and GREEN, G. J. (1967).—Reproductive potentials of races 15B and 56 of wheat stem rust. *Can. J. Bot.* **45**, 1077–91.
- LANDAHL, H. D. (1955).—A mathematical model for the temporal pattern of a population structure, with particular reference to the flour beetle. II. Competition between species. *Bull. math. Biophys.* **17**, 131–40.
- OGLE, H. J., and BROWN, J. F. (1970).—Relative ability of two strains of *Puccinia graminis tritici* to survive when mixed. *Ann. appl. Biol.* **66**, 273–9.
- OGLE, H. J., and BROWN, J. F. (1971).—Factors affecting the relative ability of strains of *Puccinia graminis tritici* to survive when mixed. *Ann. appl. Biol.* **67**, 157–68.
- PERSON, C. (1967).—Genetic aspects of parasitism. *Can. J. Bot.* **45**, 1193–204.
- PRASADA, R., ET AL. (1966).—Occurrence of physiologic races of wheat and barley rusts in India during 1957–62. *Indian Phytopath.* **19**, 45–58.
- STAKMAN, E. C., and CHRISTENSEN, J. J. (1960).—The problem of breeding resistant varieties. In “Plant Pathology: An Advanced Treatise”. (Eds. J. G. Horsfall and A. E. Dimond.) Vol. 3. pp. 567–624. (Academic Press: New York.)
- TAYLOR, N. W. (1968).—A mathematical model for two *Tribolium* populations in competition. *Ecology* **49**, 843–8.
- WATSON, I. A. (1942).—The development of physiological races of *Puccinia graminis tritici* singly and in association with others. *Proc. Linn. Soc. N.S.W.* **67**, 294–312.
- WATSON, I. A. (1958).—The present status of breeding disease resistant wheats in Australia. *Agric. Gaz. N.S.W.* **69**, 630–60.

