

Letter to the Editor Estimating Parasitic Fitness

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Generally it is conceded that some biotypes of a pathogenic species are more fit than are others. Although we understand little of the attributes of such differences, it is evident that physiological race differences are only one component of parasitic fitness. One would not expect that all isolates of *Puccinia graminis* f. sp. *tritici* race 56, for instance, would exhibit equal fitness. Other genetically controlled factors, such as aggressiveness, must contribute to an isolate's pathogenic fitness and hence to its survival and reproduction.

How then, does one measure such differences and relate them in a meaningful way to disease control procedures? These methods are the topic of this letter.

One obvious measure of parasitic fitness is the apparent infection rate (r) as discussed by van der Plank (6,7). Although van der Plank's development of r was for a mathematical description of plant epidemics, it is conceptually equivalent to the population geneticist's Malthusian parameter (1). Host cultivars for which r is measurably reduced are thought to possess horizontal resistance (5). The corresponding attributes in the parasite will herein be termed parasitic fitness and can be thought of as those differences between populations, isolates, biotypes, strains, races, etc. that are measured as differences in r when they are tested on the same host genotype under identical environmental conditions. The isolate with the higher r value then would be said to have a greater parasitic fitness. A recent article by Dovas et al. (2) provides an excellent set of data to demonstrate these methods. The selection of this data set should in no way reflect poorly on that report. The choice of this data set is intended to encourage more investigations of this type.

Estimation of parasitic fitness.—Dovas et al. (2) presented information on the epidemic buildup on sugar beets of *Cercospora beticola* strains resistant and sensitive to benomyl. The numerical values for the plotted data were obtained by using an X-Y plot digitizer measuring in 0.254-mm (0.01-inch) units. The units were converted to percent values by linear regression and are given in Table 1. When values approached 100% disease severity the entire set of paired data were omitted for these demonstrations. The frequency data of the benomyl tolerant strain (relative to the sensitive strain) were obtained by identical procedures and the values are given in Table 2.

Van der Plankian analyses of the epidemics by linear

regression of the logit-transformed values for the unsprayed plots inoculated with the (i) sensitive strain and the (ii) resistant strain gave apparent infection rates (r) of 0.070 and 0.096 units/day, respectively, quantifying, as the authors hypothesized, that the "sensitive strain, which happened to be used in the experiment, was less fit pathogenically than was the particular resistant strain with which it was compared" (2).

The intentional applications of benomyl also affected the parasitic fitness of the isolates as measured by the apparent infection rate, which is shown in Fig. 1 and 2. In Fig. 1, I have plotted the two epidemics for the sensitive strain as the logit of disease proportion over time (in days). The suggested effect of benomyl treatment was to reduce the parasitic fitness from 0.070 to 0.041 and reduce the y-axis intercept from approximately -2.0 to -4.0 . Similar effects, if attributable to the host genetics, would be considered horizontal resistance (reduced r) and vertical resistance (reduced X_0) by van der Plankian terminology.

Plots of the logit of disease proportion against time for the resistant strain are given in Fig. 2. Again, benomyl reduced the expressed parasitic fitness of the resistant

TABLE 1. Amount of disease expressed as a proportion* of *Cercospora* leaf spot of sugar beet caused by *Cercospora beticola* in two plots, one sprayed with benomyl and the second non-sprayed, for plots artificially inoculated with benomyl-sensitive or resistant or as a mixture of sensitive and resistant conidia (From Dovas et al., *Phytopathology* 66:1452-1456)

Type of epidemic	Time (days)	Disease proportion in plots	
		Benomyl-sprayed	Nonsprayed
Benomyl-sensitive strain	0	0.02	0.13
	20	0.04	0.27
	36	0.07	0.65
Benomyl-resistant strain	0	0.10	0.10
	20	0.19	0.27
	36	0.42	0.79
Mixture	0	0.03	0.06
	20	0.06	0.21
	36	0.13	0.72

*Disease proportion is an expression of severity varying between 0.00 and 1.00 with zero representing no disease and 1.00 representing a totally diseased plant population.

isolate (r dropped from 0.096 for the unsprayed epidemic to 0.052 for the benomyl-treated epidemics). It did not reduce the y-axis intercepts (-2.42 vs. -2.29) as was previously evident for the sensitive strain.

The data in Fig. 3 for the epidemics of the mixture of both benomyl-sensitive and -resistant strains support the conclusions for the separate epidemics. The benomyl-treated mixed strains epidemic suggested a reduced apparent infection rate (r fell from 0.100 to 0.046) and a lowered y-axis intercept (X_0 dropped from approximately -2.9 to -3.6), which suggested that the effect of benomyl on this epidemic, as expected, was two separate effects.

Estimation of relative parasitic fitness.—In addition to estimates of parasitic fitness, one also can estimate relative parasitic fitness from the data on the proportions of resistant and sensitive isolates over the time sampled. Employing the population genetics model for biological fitness (F) we can state that:

$$q = q_0 (F^t)$$

which says that the expected proportion (q) of a population will increase (or decrease) from the original proportion (q_0) by some coefficient of fitness (F) to some

power of the time units (t). It is convenient for plant pathologists to use time in days although geneticists commonly measure F in generations. A second modification of this model is to express the quantity of disease of the relatively less fit population (q) in terms of the relatively more fit population (p) such that the above equation becomes:

$$\frac{q}{p} = \frac{q_0}{p_0} (W^t)$$

where, using the notation from above, p and p_0 represent the proportion of the relatively less fit population (i.e., decreasing in relative frequency) at two points in time. The value of W would be the relative fitness of the less-fit population. Note that this standardization technique sets the relative parasitic fitness (W) of the relatively more fit population at 1.0 when using proportions since $p/p = 1.0$. This method of expressing data is the essence of all relative fitness analyses. Previous methods which have been suggested for analysis of parasitic fitness as applied to plant pathogens (see 3, 4, 7) have failed to stress this necessary relationship.

Regression analysis of proportion data is simplified by the observation, noted by Crow and Kimura (1) that $W = e^b$, and when

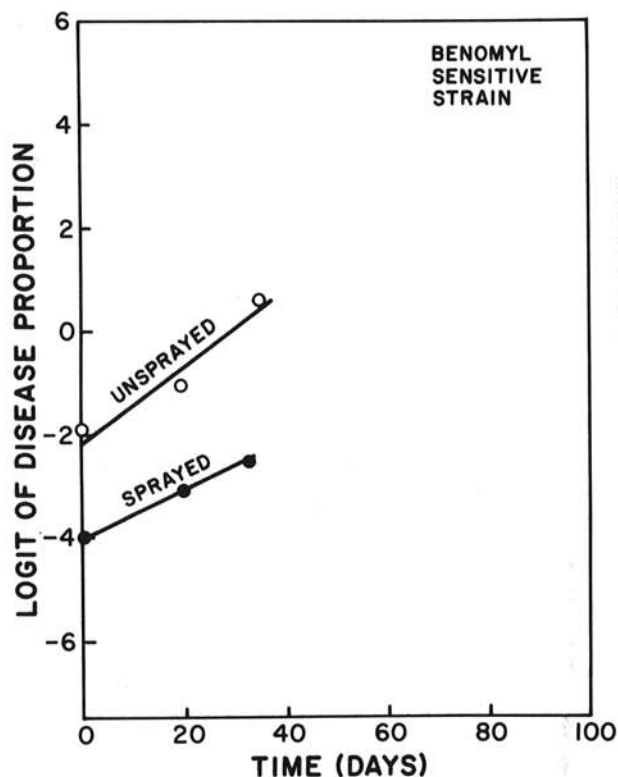


Fig. 1. Logit-transformed data for disease intensity of *Cercospora* leaf spot of sugar beet for two epidemics (one sprayed with benomyl, one unsprayed) for a strain of *Cercospora beticola* sensitive to benomyl. Apparent infection rates (r) are given as 0.070 for the unsprayed and 0.041 for the benomyl-sprayed plot with coefficients of determinations of 95.2% and 99.8%, respectively. (Data of Dovas et al., *Phytopathology* 66:1452-1456.)

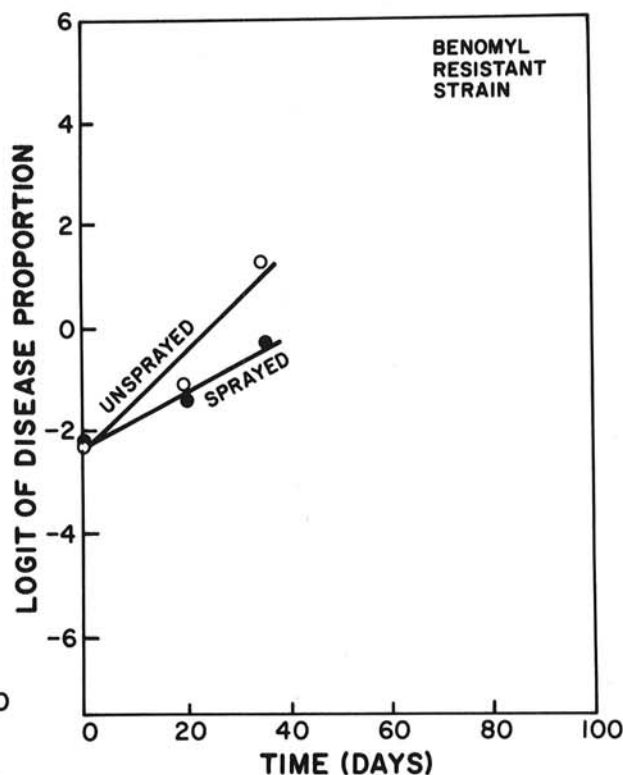


Fig. 2. Logit-transformed *Cercospora* leaf spot of sugar beet intensity for two epidemics (one sprayed with benomyl, one unsprayed) for a strain of *Cercospora beticola* resistant to benomyl. Apparent infection rates (r) are given as 0.096 for the unsprayed and 0.052 for the benomyl-sprayed plot with coefficients of determination of 03.9% and 96.4%, respectively. (Data of Dovas et al., *Phytopathology* 66:1452-1456.)

TABLE 2. Proportion of benomyl-tolerant isolates of *Cercospora beticola* of sugar beet relative to the sensitive strain in plots, one sprayed with benomyl and the second nonsprayed, for plots artificially inoculated with benomyl-sensitive or resistant or as a mixture of sensitive and resistant conidia (From Dovas et al., *Phytopathology* 66:1452-1456).

Type of epidemic	Time (days)	Proportion of benomyl-tolerant strain in plots	
		Benomyl-Sprayed	Unsprayed
Benomyl-sensitive strain	0	0.04	0.02
	12	0.53	0.06
	36	0.93	0.17
	50	... ^b	0.24
Benomyl-resistant strain	0	0.99	0.99
	12	1.00	0.96
	34	1.00	0.99
	50	... ^b	... ^b
Mixture	0	0.19	0.27
	12	0.88	0.23
	34	0.99	0.47
	50	... ^b	0.62

^bData not given.

$q = q_0 (W^t)$, then by substitution,

$$q = q_0 e^{rt}$$

which is the expression for a continuously compounded growth model where e is the base of the natural log system and r is the rate of exponential growth of that population.

When we standardize q by p , and q_0 by p_0 we can re-express p and p_0 as $1-q$ and $1-q_0$, respectively, because the frequencies are expressed as a proportion (i.e., $p + q = 1.0$). This relationship is then given as:

$$\frac{q}{1-q} = \frac{q_0}{1-q_0} e^{rt}$$

and can be made linear by natural log transformation to:

$$\ln \frac{q}{1-q} = \ln \frac{q_0}{1-q_0} + rt$$

for simple linear regression analysis of the logit-transformed proportions

$$\left(\ln \frac{q}{1-q} \right).$$

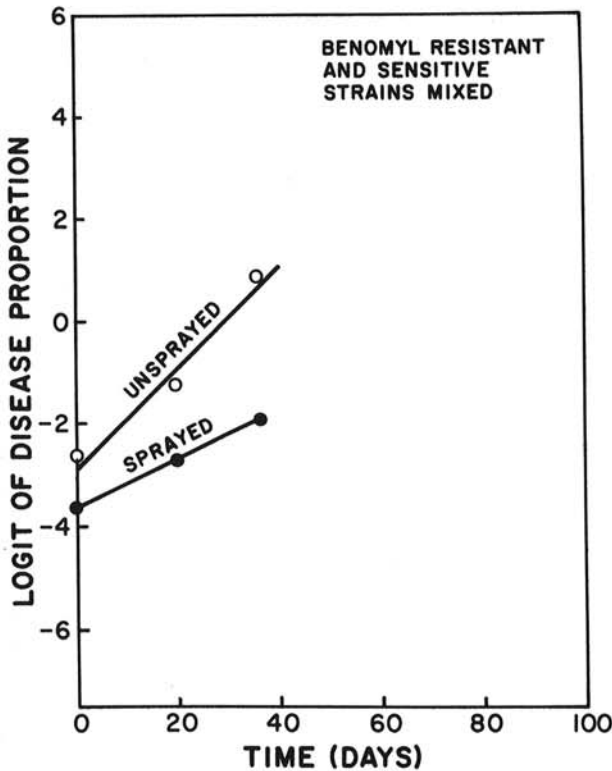


Fig. 3. Logit-transformed data for disease intensity of *Cercospora* leaf spot of sugar beet for two epidemics (one sprayed with benomyl, one unsprayed) for two strains of *Cercospora beticola*; one resistant and one sensitive to benomyl. Apparent infection rates (r) are given as 0.100 for the unsprayed and 0.046 for the benomyl-sprayed plot with coefficients of determination of 95.6% and 99.4%, respectively. (Data of Dovas et al., *Phytopathology* 66:1452-1456.)

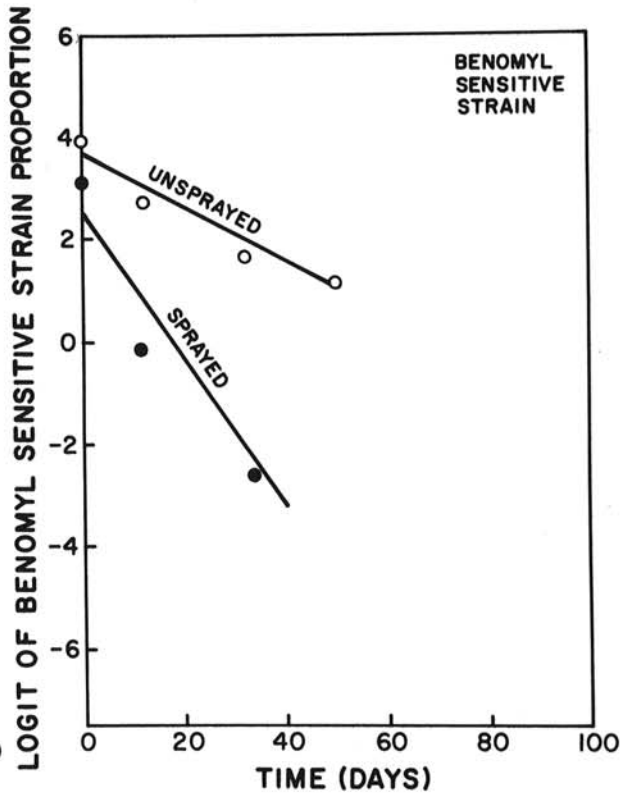


Fig. 4. Logit transformation of the proportion of benomyl-sensitive strain frequency of *Cercospora beticola* on sugar beet for two epidemics; one sprayed with benomyl and one unsprayed. Relative parasitic fitness estimates (W) for the benomyl-sensitive strain are given as $W = 0.946 (= e^{-0.055})$ for the unsprayed and $0.852 (= e^{-0.166})$ for the benomyl-sprayed plot with coefficients of determination of 94.5% and 93.6%, respectively. (Data of Dovas et al., *Phytopathology* 66:1452-1456.)

The equation also can be solved for r giving.

$$r = \frac{1}{t} \left(\ln \frac{q}{1-q} - \ln \frac{q_0}{1-q_0} \right)$$

which, except for symbol differences, is equivalent to van der Plank's apparent infection rate equation (6):

$$r = \frac{1}{t} \left(\ln \frac{x}{1-x} - \ln \frac{x_0}{1-x_0} \right)$$

Figures 4 and 5 present the transformed data of the strain proportions given in Table 2. Regression analyses on the two sensitive strain epidemics (with and without benomyl) gave linear regression coefficients (r) of -0.160 units/day for the benomyl-treated epidemic and -0.055 for the untreated epidemic. The relationship of r and w can be seen from:

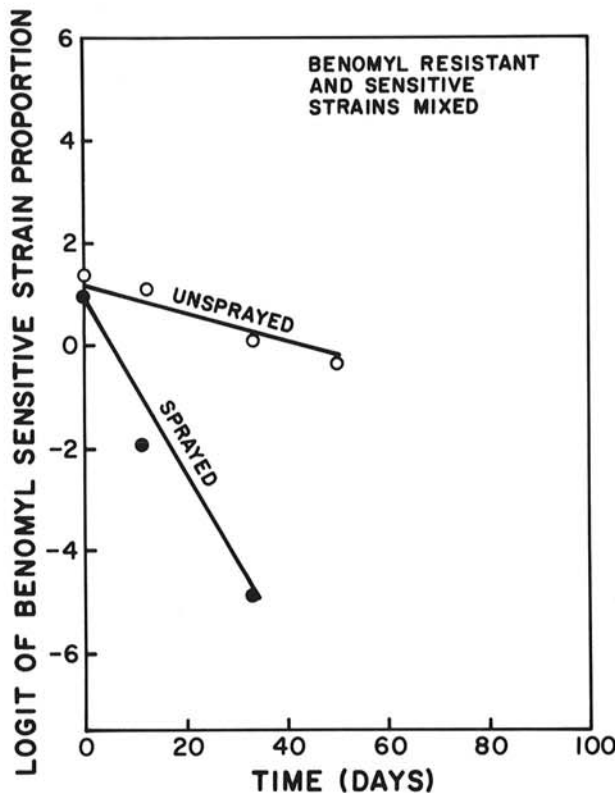


Fig. 5. Logit transformation of the proportion of benomyl-sensitive strain frequency of *Cercospora beticola* on sugar beet for two epidemics; one sprayed with benomyl and one unsprayed, for an epidemic of two strains; one sensitive and one resistant to benomyl. Relative parasitic fitness estimates (W) for the benomyl-sensitive strain are given as $W = 0.968 (= e^{-0.033})$ for the unsprayed and $0.840 (= e^{-0.174})$ for the benomyl-sprayed plot with coefficients of determination of 89.1% and 94.6%, respectively. (Data of Dovas et al., *Phytopathology* 66:1452-1456.)

$$W = e^r$$

$$\text{or}$$

$$\ln W = r$$

where W indicates the relative parasitic fitness of the less fit strain.

The relative parasitic fitness (W) of the sensitive strain was 0.852 units/day ($= e^{-0.160}$) with the benomyl spray program and 0.946 units/day for the unsprayed epidemic, indicating that benomyl also reduced the relative parasitic fitness of the sensitive strain.

The relationship of W to another genetic parameter can be easily obtained. The coefficient of selection (S) is defined as $1-W$ which gives $S = 0.148$ units/day for the benomyl-sprayed epidemic (i.e., $1.0 - 0.852$) and 0.054 units/day for the untreated epidemic.

Similar calculations were made for the mixed-strains epidemics. The calculated r values were -0.174 units/day and -0.033 units/day for the benomyl-sprayed and unsprayed epidemics, respectively. Converting r to W for the relatively less-fit sensitive strain gives a relative parasitic fitness of 0.840 units/day for the benomyl-sprayed and 0.968 units/day for the unsprayed plots. Coefficients of selection (S) for the sensitive strain for the two epidemics were then 0.160 units/day (sprayed) and 0.032 units/day (unsprayed).

It is evident from inspection of the data of Dovas et al. (1) that calculation of the relative parasitic fitness for the "resistant strain only" epidemic would not be appropriate since the resistant strain predominated throughout both the sprayed and unsprayed epidemics.

There is a mathematical link between an absolute and a relative measure of parasitic fitness that deserves mention. If one knows the parasitic fitnesses (apparent infection rates) of two isolates and would like an expression of the relative parasitic fitness (W) all one needs to do is to subtract the larger r from the smaller r (less fit isolate). This difference would be, obviously, a negative decimal. When converted to W (i.e., e^{-}) one would have, when measured without error, the relative parasitic fitness (W) of the less-fit isolate (the more-fit isolate would have, of course, $W = 1.0$).

To demonstrate this relationship with the data of Dovas et al. (2), I have calculated the relative parasitic fitness for the separate unsprayed epidemics of the sensitive and resistant strains as the difference between the apparent infection rates (calculated as before) as $0.070 - 0.096 = -0.026$ units/day. Conversion of this value to the relative parasitic fitness (W) gives 0.974 units/day and a selection coefficient (S) of 0.026 units/day for the sensitive strain relative to the resistant strain. Note that these estimates are for the two separate, unsprayed epidemics. They can be tested with the observed values for the unsprayed epidemics intentionally inoculated with both strains. Figure 5 plots the unsprayed, mixed strain proportions and gives the measured relative parasitic fitness (W) as 0.968 units/day which agrees closely with the estimated value above of 0.974 units/day. The selection coefficient (S) also, as expected, agrees closely as 0.032 units/day measured vs. 0.026 units/day for the calculated method above. Poorer agreement between the calculated and measured methods for the benomyl-sprayed comparisons were expected because, as the authors noted, significant amounts of the benomyl-

resistant strain were detected in the "sensitive strain only" epidemic. Correcting the epidemic progress curves for the "sensitive strain" epidemic with the proportions of sensitive strain recovered gives a calculated relative parasitic fitness (W) of 0.891 units/day and a coefficient of selection (S) of 0.109 units/day. Again, from Figure 5 the measured W values of 0.840 units/day and S of 0.160 units/day correspond nicely with the calculated values.

As our science becomes more sophisticated in its attempts to manage plant pathogen populations, intelligent gene deployment schemes will demand a greater understanding of pathogen fitness. I see the application of these analytical techniques as complementary to those of van der Plank's (6, 7) analysis of epidemics. Workers in our profession have for decades, mixed isolates for study to determine which is the better competitor. The techniques outlined herein quantify these relationships and allow for the application of regression theory to the measurement of parasitic fitness.

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