Linear Models to Estimate Relative Fitness: A Reply

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Accepted for publication 24 February 1998.

Sun and Zeng (6) proposed a linear model to estimate the relative fitness of plant pathogens in cultivar mixtures. The linear model was considered “wrong” by Østergård and Shaw, supported critically by a proof of numerical validation (5). Because Sun and Zeng’s model is the first to estimate relative fitness of pathogens in a cultivar mixture for practical use, it is worthwhile to examine Østergård and Shaw’s critique carefully. We have found that Østergård and Shaw’s numerical approach to evaluate pathogen fitness is biologically and mathematically sound. However, they have incorrectly applied their approach to evaluate Sun and Zeng’s model, which resulted in an erroneous conclusion. This letter shows that Østergård and Shaw improperly cross-validated two systems that are defined over different ranges of values, a flaw not uncommon in plant pathology literature of quantitative analysis. We also propose an alternative method to calculate overall fitness value in a cultivar mixture.

On Østergård and Shaw’s validation. Sun and Zeng (6) described relative fitness by using a simple system of two pathogen genotypes (they called races), 1 and 2. The relative fitness, f , is calculated using frequencies of the genotypes at the beginning of a season (p_{10} and p_{20}) and at the end of the season (p_1 and p_2) as

$$f_{12} = (p_1/p_2)/(p_{10}/p_{20}) \quad (1)$$

in which the more fit genotype (race) is always designated as genotype 2, so the value of f is never larger than 1 (6). The allowed range of values for the fitness is thus $0 \leq f_{12} \leq 1$. They further extended their definition to a pathosystem with at least two genotypes in m cultivars of mixture. The relative fitness of the i th genotype to the j th genotype is expressed with a linear model:

$$(p_i/p_j)/(p_{i0}/p_{j0}) = c_1 f_{ij1} + c_2 f_{ij2} + \dots + c_m f_{ijm} \quad (2)$$

in which f_{ijk} ($k = 1$ to m) is fitness of the i th genotype relative to the j th genotype on cultivar k , and c_k is the proportion of cultivar k in the cultivar mixture. They again defined the allowed range of values for overall fitness in a cultivar mixture in 0 to 1 using a condition that “The race with the greatest fitness, if known, is designated the j th race” (6). Since f_{ijk} is no larger than 1, $c_k f_{ijk}$ is no larger than c_k . Because the sum of $c_1, c_2, \dots, c_m$ equals 1 and $c_k f_{ijk} < c_k$, the overall relative fitness of the i th genotype relative to the j th genotype should be no larger than 1 (6).

The fitness in Østergård and Shaw’s (5) system has a definition region different from that of Sun and Zeng’s (6) system. The absolute fitness, v , was introduced, and v_i of the i th genotype is defined as the average number of spores produced from spores present at the beginning of the season. Therefore, in a two-genotype situation, the fitness of genotype 1 relative to genotype 2 is

$$f_{12} = v_1/v_2 \quad (3)$$

With Equation 3, one can also calculate the fitness of genotype 2 relative to genotype 1 as $f_{21} = v_2/v_1$. Because v_i and v_j range from 0 to ∞ (infinity), the fitness value of $f_{ij} = v_i/v_j$ is in the region of 0 to ∞ .

The problem with Østergård and Shaw’s (5) evaluation of Sun and Zeng’s (6) model is the direct interchange of values between two systems that are different in definition regions. Østergård and Shaw (5) first have a hypothetical two-cultivar mixture, in which two pathogen genotypes have equal frequencies at the beginning and at the end of the season. They first calculated the spore densities at the end of a season and then the relative fitness values of each genotype relative to the other on two cultivars. Here, we call these component fitness values, and these values are 2 and 0.5 for the first genotype and 0.5 and 2 for the second genotype. By substituting these values into Sun and Zeng’s (5) model (5), which had a definition region of 0 to 1, Østergård and Shaw (5) obtained “a relative fitness of $0.5 \times 2 + 0.5 \times 0.5 = 1.25$ for either genotype. Østergård and Shaw, when expecting a value = 1 for two equal genotypes, obtained 1.25, which led them to conclude that the result calculated with Sun and Zeng’s linear model is “clearly nonsense”.

Mathematically, one cannot directly cross-validate two systems that are different in definition regions (1). If we make a cross-validation using component fitness as inputs, of which the region does not match the region for model output, results can be misleading. When Østergård and Shaw’s component fitness values (region 0 to ∞ , such as $f = 2$ for fitness value of genotype 2) were used as inputs to calculate overall fitness with Sun and Zeng’s model, which was defined in region 0 to 1, Østergård and Shaw were bound to draw an incorrect conclusion. Actually, the results from Østergård and Shaw’s calculation further prove the usefulness of Sun and Zeng’s linear model. The fact that the two genotypes have equal overall fitness values (1.25) means the genotypes are equal in fitness if the model output (overall fitness) is also defined in the region of 0 to ∞ . Obviously, Østergård and Shaw’s criticism of Sun and Zeng’s model is not warranted.

An alternative method. Although models proposed by both schools have merits, they both have practical limitations in terms of application. For example, in a wheat rust system, the application of Østergård and Shaw’s model would require one to quantify the average number of spores of each genotype in spore clouds at the beginning and the end of a season. This information may be more difficult to obtain than the relative genotype frequencies necessary to apply Sun and Zeng’s model. However, use of Sun and Zeng’s model requires that one particular genotype has the greatest fitness on each and every cultivar. This condition may be difficult to meet when the number of cultivars and rust genotypes is large. Rather than choosing a method of averaging “fitness” for mere convenience of calculation, we propose an alternative approach based on the original meaning of the term.

To clearly state the problem, it is necessary to start with a clean slate and define the terminology. The real problem is what do we

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Publication no. P-1998-0320-020

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mean by the terms “fitness,” “absolute fitness,” and “relative fitness?” How are these definitions affected by the details of each experiment? What is the consistent and biologically meaningful way to average over experiment to obtain “overall fitness” and “overall relative fitness?” Once the aforementioned terms are defined, the rest will follow and the relative importance and meaning of each approach (5,6) will be clear.

The simplest way to define fitness is in analogy with the one isolate-one cultivar example in which fitness, F , is defined in terms of the ratio of the final to the original pathogen population:

$$F^t = \frac{P(t)}{P(t=0)} \quad (4)$$

For a set of experiments taking place over the same time scale, it is convenient to set the value of either side of Equation 4 to a new variable, v (“absolute fitness” sensu Østergård and Shaw [5]). If P_{ik} and P_{ik0} represent the final and initial populations, respectively, of pathogen i on host k , then

$$v_{ik} = \frac{P_{ik}}{P_{ik0}} \quad (5)$$

It is this basic definition of v as a ratio that causes problems with averaging, since the ratio of the sum of a set of numbers is not equal to the sum of the individual ratios. This definition can be unambiguously extended to any number of pathogens on any number of hosts by always using ratios of true population numbers in lieu of population frequencies ($p_{ik} = P_{ik}/\sum_j P_{jk}$). The confusion in taking the mean of Equation 5 is increased if the populations are expressed as frequencies (another ratio). The answer to this dilemma cannot be found through algebra, but rather by clearly defining what is meant by the term “overall fitness.” If one is to maintain the biological notion that “overall fitness,” v , represents a ratio of initial to final population, then the average must be defined as the ratio of the sums. Thus, the “overall fitness” of an isolate reared on a number of cultivars is simply the sum over all the cultivars of the final population of the isolate divided by the sum over all the cultivars of the initial population,

$$\bar{v}_i = \frac{\sum_k c_k P_{ik}}{\sum_k c_k P_{ik0}} \quad (6)$$

in which c_k represents the proportion of the total host plants that are of cultivar k . Note that Equation 6 does not agree with the weighted average of ratios proposed by Østergård and Shaw (5):

$$(\bar{v}_i)_{O\&S} = \sum_k c_k v_{ik} = \sum_k c_k \frac{P_{ik}}{P_{ik0}} \neq \frac{\sum_k c_k P_{ik}}{\sum_k c_k P_{ik0}}$$

Agreement between $(\bar{v}_i)_{O\&S}$, defined above, and Equation 6 occurs only if the initial population of a particular genotype is exactly the

same on each and every host cultivar. Likewise the “overall fitness” of all the pathogen strains on cultivar k is

$$\bar{v}_{..k} = \frac{\sum_i P_{ik}}{\sum_i P_{ik0}} \quad (7)$$

and the “overall fitness” for all strains on all cultivars is

$$\bar{v}_{..} = \frac{\sum_i \sum_k c_k P_{ik}}{\sum_i \sum_k c_k P_{ik0}} \quad (8)$$

Perhaps the logic in using the ‘ratio of the sums’ in taking the above averages can be made more transparent through the use of an analogous example. The most commonplace variable defined as a ratio is velocity (V), the ratio of distance traveled to elapsed time. Consider the following allegorical automobile ride covering a distance of 26 km. The trip starts with a 10-min period of city driving at a velocity of 48 km/h. Perhaps one is then stopped at a construction site ($V = 0$) for a total of 8 min, after which a final 12-min jaunt on the highway at 90 km/h completes the journey. Although the average velocity for this trip can be calculated through a rather involved weighted average over each individual velocity, it is much simpler to take the total distance covered (26 km) and divide by the total elapsed time (30 min = 0.5 h). Thus, for this case, the average velocity is 52 km/h (26/0.5).

With these definitions of “overall fitness” (Equations 6 to 8), “overall relative fitness” can be defined in its original sense (1,2, 3,4). Equation 6 takes on a maximal value for one of the pathogen genotypes, say genotype j . Then we define the “overall relative fitness” for genotype i with respect to genotype j , f_{ij} , as

$$f_{ij} = \frac{\sum_k c_k P_{ik} \sum_k c_k P_{jk0}}{\sum_k c_k P_{ik0} \sum_k c_k P_{jk}} \quad (9)$$

We note that the value of f_{ij} is always between 0 and 1. One can manipulate Equation 9 to express f_{ij} in terms of relative population frequencies.

ACKNOWLEDGMENTS

We thank J. Groth, K. Leonard, and S. Sanogo for critically reviewing the manuscript.

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