

Comments on the van der Kamp-Tait Susceptibility Model for Resistance Selection

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van der Kamp and Tait (3) developed a mathematical model to describe the lodgepole pine (*Pinus contorta* Douglas ex Loud.)-western gall rust (*Endocronartium harknessii* (J.P. Moore) Y. Hiratsuka) pathosystem. Although discussed in terms of this particular disease, the model concerns itself with the segregation of members of a natural population that are susceptible and resistant to diseases characterized by discrete infections. van der Kamp (2) applied the model to investigate the theoretical limits of selecting trees for resistance to a particular disease and concluded that "...the ability to identify resistant trees is significantly compromised by random placement of spores and by the large number of trees that remain uninfected". In contrast, our examination of the model predicts increased levels of resistance when disease-free trees are selected.

The first model assumption is that for a single population the proportion of plants in each of $N + 1$ susceptibility classes is described by the binomial distribution

$$b_i(N, p) = \binom{N}{i} p^i (1-p)^{N-i} \quad (1)$$

where N and p are the binomial parameters and i is the class index that ranges from 0 to N corresponding to increasing susceptibility. This is equation 1 in van der Kamp and Tait (3). The second model assumption is that the susceptibilities of the classes are related to each other by either an additive or a multiplicative relationship:

$$S_{i+1} = S_0 + iB \quad (2)$$

or

$$S_i = S_0 B^i \quad (3)$$

where B is the increment parameter and S_0 is the susceptibility of the least susceptible (most resistant) class. These are equations 4a and b in van der Kamp and Tait (3). The third model assumption is that the distribution of the number of infections per tree for trees belonging to the i th susceptibility class is described by a Poisson distribution:

$$P_i(X) = \exp(-\lambda_i) \lambda_i^X / X! \quad (4)$$

where X is the number of infections and the Poisson parameter $\lambda_i = DS_i$, where D is the dosage and S_i is the susceptibility at "unit dosage" (3).

van der Kamp and Tait (3) chose N to be 20 and calculated the predicted number of discrete infections. A minimization technique was used to generate chi-square statistics, and the multiplicative

relationship, rather than the additive relationship, gave the closest fit with their data. For the multiplicative case, their procedure gave values for p , B , and S_0 of 0.824, 3.21, and 9.85×10^{-10} , respectively.

With the estimate of p , the left side of equation 1 can be computed for each class. These b_i values are given in Table 1 and are illustrated in Figure 1. Figure 1 corresponds to Figure 2 in van der Kamp and Tait (3) or to the hatched bars in Figure 1 in van der Kamp (2). By substituting the estimated values of B and S_0 into equation 3, the susceptibility for the i th class is obtained (Table 1).

For each class (or bar in Fig. 1), the proportion of trees with 0 infections can be computed from the Poisson distribution. This proportion (corresponding to $X = 0$) is determined by substituting the values of $\lambda_i (=DS_i)$ into equation 4, remembering that $\lambda^0 = 1$ and $0! = 1$. The resulting values of $P_i(0)$ (Table 1) show that all trees with 0 infections originate from classes with susceptibilities less than or equal to 0.402. Equivalently, these trees come from classes that have fewer than an average of 2.01 ($DS_i = 5 \times 0.402$; Table 1) infections per tree when the population average is 5 infections per tree. Thus, the ability to identify resistant candidates is improved by selecting trees with 0 infections.

We now have the proportion of trees in each class that has 0 infections and the proportion of trees in the whole population repre-

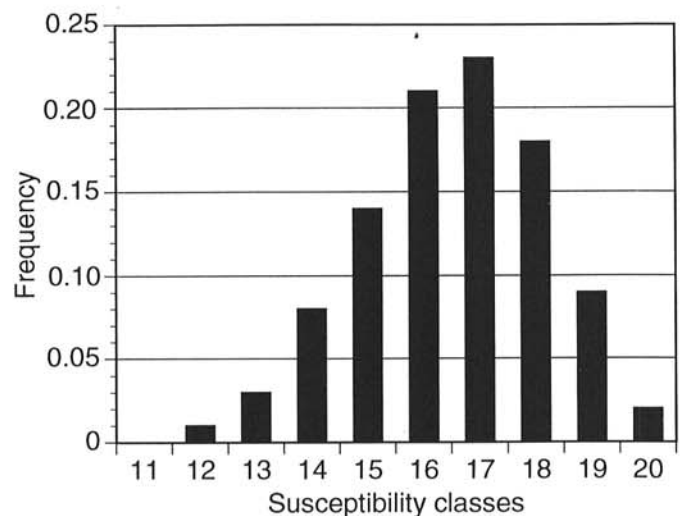


Fig. 1. Proportion of trees (lodgepole pines) in each susceptibility class from a natural population segregated for susceptibility to a plant disease (western gall rust). The proportions are calculated from the binomial distribution (equation 1 in text) and are listed in Table 1. Proportions in classes 0 to 10 are too small to graph.

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TABLE 1. Values calculated for model variables and parameters from the lodgepole pine-western gall rust data of van der Kamp and Tait (3)

Parameter	Susceptibility class ^a									
	11	12	13	14	15	16	17	18	19	20
b_i^b	0.00	0.01	0.03	0.08	0.14	0.21	0.23	0.18	0.09	0.02
S_i^c	0.000	0.001	0.004	0.012	0.039	0.125	0.402	1.290	4.140	13.290
$DS_i^d (D = 5)$	0.00	0.01	0.02	0.06	0.19	0.63	2.01	6.45	20.70	66.45
$P_i(0)^e$	1.00	0.99	0.98	0.94	0.82	0.53	0.13	0.00	0.00	0.00
$b_i P_i(0)^f$	0.00	0.01	0.03	0.07	0.12	0.11	0.03	0.00	0.00	0.00
$b_i P_i(0)/T^g$	0.01	0.03	0.08	0.19	0.31	0.29	0.08	0.00	0.00	0.00

^a Classes 1 to 10 are not shown because their susceptibilities are too small to contribute to the calculations.

^b b_i is the proportion (binomial probability) of trees in the i th class computed from equation 1 (in text).

^c S_i is the susceptibility of the i th class computed from equation 3 (in text), with values of B and $S_0 = 3.21$ and 9.85×10^{-10} , respectively.

^d DS_i is the Poisson parameter, λ_i , for the i th class.

^e $P_i(0)$ is the proportion of trees with 0 infections in the i th class computed from equation 4 (in text).

^f $b_i P_i(0)$ is the nonstandardized proportion of trees with 0 infections in the i th class.

^g $b_i P_i(0)/T$ is the standardized proportion of trees with 0 infections in the i th class; $T = \sum_{i=1}^{20} b_i P_i(0)$.

sented by each class. By multiplying $P_i(0)$ by b_i , one obtains the nonstandardized proportions of trees with 0 infections from the whole population within each class (Table 1). This set can be standardized by summing the elements in the set and dividing each member by the sum ($T = 0.37$) to obtain the results listed in Table 1: $P_i(0)b_i/T$; $T = [P_0(0)b_0 + \dots + P_{20}(0)b_{20}]$. These numbers mean, for example, that 19% of the trees with 0 infections (Table 1) come from the class in which there is an average of 0.06 (DS_i ; Table 1) infections per tree, and 31% of the trees with 0 infections come from the class in which there is an average of 0.19 infections per tree when the overall population average is 5 infections per tree. These percentages show that more than 90% ($1 + 3 + 8 + 19 + 31 + 29 = 91 = 100 \sum_{i=0}^{16} b_i P_i(0)/T$; Table 1) of the trees with 0 infections come from susceptibility classes with 0.63 or fewer (DS_i ; Table 1) infections per tree when the overall average is 5 infections per tree.

If the experiment could be repeated several times, not all the trees with 0 infections in one experiment would necessarily have 0 infections in all other experiments. The expected number of infections on trees with 0 infections can be determined by multiplying the proportions given by $b_i P_i(0)/T$ in Table 1 by the susceptibility of the class to which they correspond (S_i), summing, and multiplying by 5. The resulting 0.43 infections per tree is an order of magnitude improvement over the population average of 5 infections per tree for this data set (2,3). Therefore, in contrast to van der Kamp and Tait (3), we believe that selection of trees with 0 galls will result in a significant improvement in resistance and that the ability to identify resistant trees is not significantly compromised by random placement of spores (2).

In Figure 2, which corresponds to Figure 2 in van der Kamp (2), the top or heaviest line is the average susceptibility (weighted by b_i) of trees with 0 infections plotted against severity of disease in the population, defined as the average number of infections per tree. The points used to plot this line were obtained by computing the expected number of infections on trees with 0 infections for each value of D from 1 to 50 according to the procedure used above and then dividing by D to obtain the susceptibility of the infection-free trees. For example, if the average number of infections per tree in the whole population is 5, one obtains the average susceptibility of the trees with 0 infections from the heaviest (top) line by reading the y value that corresponds to an x value of 5 in Figure 2. Multiplying this y value (0.085) by 5 gives 0.43, which is the value obtained previously.

One could now pose the following question. If it were possible to identify the class to which a disease-free tree belonged, what sort of improvement in resistance might one expect from this selection, or conversely, what is compromised by not knowing the class of the disease-free tree? This can be calculated by establishing a threshold so only disease-free trees from classes with susceptibilities below the specified threshold are included. In Figure 2, the bottom three lines correspond to trees with 0 infections that

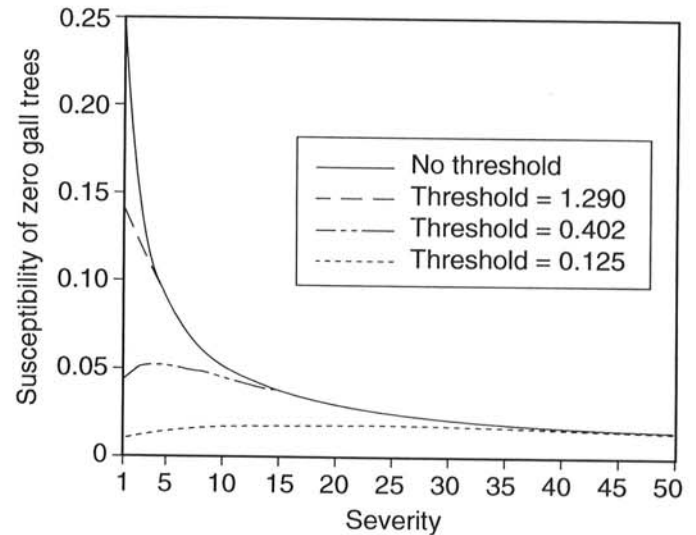


Fig. 2. Susceptibility of individual trees (lodgepole pines) with 0 infections for severities (average number of infections per tree in the population) ranging from 1 to 50 infections per tree for western gall rust data. The top line includes all 0-infection trees from all classes. The second line includes all 0-infection trees from classes with susceptibilities below 1.290, i.e., class 17 or lower. The third line includes all 0-infection trees from classes with susceptibilities below 0.402, i.e., class 16 or lower. The fourth line includes all 0-infection trees from classes with susceptibilities below 0.125, i.e., class 15 or lower. Susceptibility is defined as the number of infections per tree when the population average is standardized to 1 infection per tree.

originate from classes with susceptibilities below the specified thresholds. The susceptibility and expected number of infections for disease-free trees selected from classes with susceptibilities less than a threshold of 0.402, corresponding to the third line from the top in Figure 2, are 0.052 and 0.26, respectively, when the severity of disease in the population is 5 infections per tree. Therefore, even if one knew the classes from which the disease-free trees originated, the values differ in this case by 0.17 of an infection (from 0.26 to 0.43). Consequently, in our view, not being able to identify the susceptibility classes from which the disease-free trees originate is not a significant compromise.

The original model refers to a set of "uninfected trees...more resistant than any of the infected trees" (2; Fig. 2) based on the concept of selection with "perfect knowledge." However, it is evident from Figure 1 and Table 1 that such a set of uninfected trees cannot be selected, even if perfect knowledge is invoked. Given a tree with 0 infections that originates from the class with susceptibility of 0.125, for example, one can always find an infected tree from a class with a lower susceptibility, 0.039 for example. This is because each class contains trees that are both infected and not infected. Thus, given a subpopulation of uninfected trees, it is always possible to find an infected tree that is more resistant than

some of the trees in the subpopulation, so a set of uninfected trees in which every individual is more resistant than any of the infected trees does not exist.

What one can do with perfect knowledge is select uninfected trees that have a susceptibility less than any uninfected trees that are not selected. The threshold susceptibility used above allows selection of only those uninfected trees that come from classes with known susceptibilities. Illustrated in Figure 2 are examples of the curves that result for three different thresholds. Thus, one can choose a threshold that results in a line being closer to the topmost line (a smaller compromise to use van der Kamp's term [2]) or further away (a larger compromise), but in any case, the absolute maximum for the compromise is only 0.43 infections per tree when the average is 5 infections per tree.

We now examine more closely the definitions of dosage and susceptibility. In the original model (3), unit dosage is defined first as the level of effective dosage that results in an average of 1 gall per tree in the host population (3). Later, the relative susceptibility is defined as the expected number of infections on the tree at unit effective dosage (3). If a population of trees had an average of 1 infection per tree, the dosage, by definition, would automatically be unit dosage, without any reference to the concentration or amount of inoculum applied. This seems inconsistent with conventional notions of the meaning of dosage (1). We believe that using dosage and unit dosage in this context introduces unnecessary difficulties into the model.

The susceptibility for each class, S_i , is defined as the expected number of infections per tree in that class at unit dosage (3). We express this as

$$S_i = N_i^1 \quad (5)$$

where N_i^1 is the expected number of infections in the i th class at unit dosage. We denote the probability of the i th susceptibility class as p_i and, as van der Kamp and Tait do (3), the susceptibility by S . As a result, the expected susceptibility of the population is

$$E(S) = \sum_{i=0}^{20} S_i p_i = \sum_{i=0}^{20} N_i^1 p_i = 1 \quad (6)$$

by the definition of unit dosage, where E is the expectation operator.

Although van der Kamp and Tait obtained this result using the Poisson distribution in their appendix (3), it has been obtained here without making any reference to the form of the probability distribution. Regardless, equation 6 predicts that no matter what the population of trees, the expected value of the susceptibility for the population is always the same, namely 1.

This means that the model cannot be used to compare susceptibilities of two or more populations, because susceptibility is defined in the original model as the number of infections on a tree at unit dosage and unit dosage is the dosage that always gives, on average, 1 infection per tree. Imagine that two different populations of trees—one prone to infection and one not prone to infection—are inoculated under identical conditions and that the same amount of inoculum is applied to each. The dosage, in a

conventional sense, is the same, but the two populations will have a different average number of infections per tree. However, according to the definitions of dosage and susceptibility in the original model, the average number of infections per tree in both populations has been defined as the same, exactly 1.

To eliminate this difficulty, two modifications of the model definitions are suggested. First, when considering a single population, as the original model does, susceptibility can be defined as the number of infections per tree for a given susceptibility class when the population average is 1 infection per tree. If, in a field situation, the population average is different than 1 infection per tree, the susceptibility can be standardized by dividing the number of infections on a tree by the average number of infections per tree in the population. As a result, the terms unit dosage and dosage would not be needed. When susceptibilities in more than one population are compared, inoculum density and environmental conditions would be standardized. Standardization of inoculum and environment would allow comparison of different populations, and the average number of infections would not be forced to be 1. Second, in equation 4, dosage can be replaced by severity, the average number of infections per tree. For completeness, the symbol D (dosage in equation 4) can be renamed or replaced by another symbol, Q , that represents severity. With these changes, equation 4 remains, except that λ_i is now given by $\lambda_i = QS_i$.

In summary, we have used the model assumptions (the binomial distribution of susceptibility classes, the Poisson distribution for infections on a tree within a class, and the multiplicative process to relate susceptibility classes) together with the van der Kamp and Tait (3) estimates of the critical parameters (N , p , B , and S_0) to conclude that trees with higher levels of resistance can be identified and selected from a single population of trees. Selecting trees with 0 infections will yield a subpopulation with an expected number of infections per tree that is an order of magnitude smaller than the overall population average in the case in which this average is 5 galls per tree. Even with "perfect knowledge" the absolute maximum increased improvement (beyond the order of magnitude improvement already achieved) is only 0.43 infections per tree. Therefore, the ability to identify resistant trees is not "significantly compromised by random placement of spores and by the large number of trees that remain uninfected." We also have pointed out that it is unnecessary to introduce the concept of "unit dosage" and "dosage" and that the dosage in the original model is actually the "severity."

LITERATURE CITED

1. Commonwealth Mycological Institute. 1968. Plant Pathologist's Pocketbook. Lampert Gilbert Printers, Ltd., Reading, Berkshire, England.
2. van der Kamp, B. J. 1993. Limits to selection for disease resistance from natural tree populations. *Can. J. For. Res.* 23:1944-1947.
3. van der Kamp, B. J., and Tait, D. E. N. 1990. Variation in disease severity in the lodgepole pine-western gall rust pathosystem. *Phytopathology* 80: 1269-1277.