Estimating the Level of Susceptibility to *Phytophthora infestans* in Potato Genotypes

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ABSTRACT

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Resistance and susceptibility are closely related terms but differ in their underlying assumptions and measurement. Standardized methods for determining the level of resistance and susceptibility in potato to *Phytophthora infestans*, the causal agent of late blight, have traditionally been semiquantitative and are not based on a true interval scale, thus making their use in most mathematical and statistical operations inappropriate. Recently, researchers have attempted to develop interval scales using regression analysis of the direct or transformed area under the disease progress curve (AUDPC). In this article, a similar approach is described based on the relative AUDPC (RAUDPC) of one or two

reference cultivars and tested using a data set of field trials involving cultivars with varying levels of susceptibility evaluated in different environments in several countries. The coefficient of variation (CV) among trials of the AUDPC was reduced when the RAUDPC was used and even more so when the RAUDPC was made relative to the RAUDPC of cv. Bintje (RaRAUDPC), which was present in all trials. The RaRAUDPC was used in regression models to estimate scale values for eight potato cultivars in 13 to 15 locations (depending on cultivar). The CVs of scale values measuring variation among sites were similar to those of the RaRAUDPC. Using two cultivars gave a slight improvement in CV, which was statistically significant. The scale developed here has ascending numbers for increasing susceptibility, is simple, and can be constructed as a ratio measure, which permitted the calculation of mean, variance, and CV.

The susceptibility and resistance of plants to pathogens are closely related, but quantification of either relies on different assumptions. The amount of resistance is often estimated using an ascending scale corresponding to decreasing amounts of disease, where the smallest numbers represent low levels of resistance (large amounts of disease) and the largest numbers represent increased levels of resistance (small amounts of disease).

There is one fundamental problem with his approach. To quantify resistance, one assumes a baseline state of the plant where there is a minimum or no resistance, with this corresponding to the lowest value on the chosen measurement scale. However, if minimum or no resistance is defined by a high level of disease in a standard "susceptible" host genotype, one could always find another genotype with more disease, at least in theory. This, in turn, would change the baseline state of the host species and require an even lower value on the measurement scale.

An alternate approach is to estimate susceptibility. Plant pathologists often measure various aspects of disease severity (such as percent area affected or area under the disease progress curve [AUDPC]) and these numbers can be used to estimate susceptibility. The susceptibility of a plant can then be used to make inferences about its resistance. An approach estimating susceptibility is presented in this article using potato late blight as an example.

Host plant resistance in potato (*Solanum tuberosum* L.) to the late blight pathogen, *Phytophthora infestans* (Mont.) de Bary, is a potentially important factor in controlling the disease in both the temperate zone and the tropics. Some resistance phenotypes are absolute and these can be classified as race-specific or vertical resistance sensu Vanderplank (17). These can be characterized

with a simple presence or absence measure. Other phenotypes result in varying levels of susceptibility and represent what is frequently considered to be quantitative resistance (5) and, thus, require a quantitative estimate.

Even though all measurement scales can be represented as numbers, they can have different properties (16). In the simplest form, the nominal scale, the numbers merely denote individuals. An example of this would be the numbers on jerseys of a football team and, in this case, letters or words would work equally well. More information is present if numbers represent rankings (ordinal scale), such as a ranking of wines in a taste evaluation. In a third type of measurement (interval scale), the intervals between the units represent equal spacing. Stevens (16) also discussed a fourth scale (ratio scale), where the ratios are meaningful. The Celsius and Kelvin scales for temperature provide good examples of interval and ratio scales, respectively. On the Kelvin scale, the concept of zero is meaningful (giving meaning to the concept of twice as warm), whereas the zero of the Celsius scale is arbitrary. Most of the quantities that we associate with numerical measurements (such as length or temperature) are either interval or ratio scales.

The nature of the measurement scale places constraints on the types of statistical analyses that can be done with the numbers. It is easy to recognize the difficulty of interpreting the sum or mean of the numbers taken from a set of football jerseys but the mean and standard deviation of ranks is also difficult to interpret, because the intervals between the ranks may not be the same. Therefore, the use of a numerical scale for potato resistance to *P. infestans* becomes problematic if it is not an interval or ratio scale, because most mathematical and statistical operations are inappropriate with an ordinal scale and meaningless with a nominal scale.

Typically, the comparison of genotypes for resistance to *P. infestans* is done using a direct measure of disease severity, which

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may be measured at a specific time or integrated over the season (13). The most common procedure for integrating disease severity readings is to calculate the AUDPC using the midpoint method (6). The AUDPC and variants thereof have been recently used in the United States to measure resistance in potato to *P. infestans* (12,14). The AUDPC, however, is affected by many factors other than the level of host resistance and, therefore, is only applicable within a single experiment. The relative AUDPC (RAUDPC) was proposed as a standardized and, therefore, more stable measure of cultivar performance (10) but it is also subject to variation from factors that are experiment specific and, therefore, is also not appropriate for use as a measure of resistance across experiments.

Resistance to late blight in potato is classified on a 1-to-9 scale in Europe (available online by the European Potato Association), where 1 represents the most susceptible cultivars and 9 the most resistant ones. The historical development of the European scale was recently reviewed by Hansen et al. (11), who noted that the scale was first described by Malcolmsen (15) but has since been modified by several workers. Although the purpose of the scale and the use of sequential numbers both would imply that the scale is based on equal intervals, we know of no studies that have demonstrated the interval nature of the scale. Using the classification of Stevens (16), one might rather think of the units of the European scale as ordered classes (ordinal scale), in which calculations such as median and percentile might be appropriate but other simple arithmetic manipulations, such as calculating the mean, would be inappropriate. Most commonly used statistical analyses, such as analysis of variance, would also be inappropriate.

In addition to the inherent properties of the European scale, there is another problem associated with its use: no clear indication is given as to how severity values (often the AUDPC) are converted to scale values. Even when reference cultivars with known scale values are included in trials, it is not clear how scale values are assigned to test cultivars falling between reference cultivars (11). One can easily imagine how this could be a minor problem if the number of reference cultivars is large and a major problem if there are only one or a few reference cultivars.

To address some of the problems associated with the current European scale, the approach of converting disease severity data to a resistance scale was explored quantitatively by Hansen et al. (11). They estimated scale values by regressing known scale values of reference cultivars on the square root of the ratio of two RAUDPCs. In their study, the RAUDPC of each cultivar had been normalized by dividing it by that of reference cv. Oleva, and the square root of the quotient was used as the independent variable in regression analysis. The resulting regression parameters were then used to estimate resistance ratings (scale values) in the test cultivars.

Both the scale of Hansen et al. (11) and the current 1-to-9 European scale estimate resistance, where increasing numbers represent increasing resistance. The European scale seems to stem from the Dutch Rassenlijst voor Landbouwgewassen, which was then adapted by Malcolmsen (15). It is interesting to note, however, that Malcolmsen (15) compares her scale to Black's 1-to-5 scale (2), where increasing numbers represented increasing susceptibility. This was also the approach taken by Darsow (7), who used a 1-to-9 scale, with 9 representing the highest level of susceptibility. As noted earlier, the focus of measurement on resistance rather than susceptibility has consequences for the properties of the scale.

Classifying late blight resistance in potato genotypes is particularly problematic in the highland tropics, where potato late blight is a severe constraint of potato production (9). In this agroecosystem, European reference cultivars are not used and probably would not work because of poor adaptation to short day lengths. Some breeders at the International Potato Center (CIP) have selected and use reference cultivars to improve interpretation of

results (4) but the process has not been standardized throughout the center, and much less among other potato breeding programs in developing countries. No scale has been adapted for short-day conditions, and we are aware of no publications that even discuss the issue for this part of the world.

Our objective is to present one specific approach for measuring susceptibility in potato genotypes that has broad application. We also discuss the general methodology of using various disease metrics to estimate numbers that represent host plant susceptibility and resistance. We intend that our discussion will facilitate the development of suitable measures in the future.

MATERIALS AND METHODS

Analyses were performed on a data set previously collected to examine the stability of resistance to late blight in a collection of potato cultivars with different levels of horizontal resistance (8). Because our goal was to explore methods of converting disease measurements into levels of some sort of scale, a subset of the data was chosen that included only the most stable cultivars, and some problematic locations and cultivars were omitted. These edits included removing cvs. Chata Blanca, Torridon, Teena, Stirling, Pimpinel, and Monserrate due to strong interaction effects in one or more of the trials. All the trials from Ecuador and Argentina also were excluded because of large genotype–location interactions identified in the previous study. One trial each from the United States (trial 2) and Denmark (trial 3) were also excluded based on interactions evident in the biplots presented in the original article (8).

A number of disease measures were analyzed for developing the resistance scales. Some measures could be calculated from data of a single cultivar. These included the AUDPC and RAUDPC. Other measures that were explored required data from two cultivars. One was the ratio of two RAUDPCs (one from the cultivar of interest and the other some standard cultivar), referred to here as RaRAUDPC. This is numerically equivalent to the ratio of two AUDPCs, because the maximum possible AUDPC is the same for all genotypes in one trial. Analysis was also done with the square root of the ratio of two RaRAUDPCs, because Hansen et al. (11) used this disease measure in their study of 1-to-9 resistance scales.

Analysis strategy. The first step in the analysis strategy involved selection of the most appropriate disease measure (AUDPC, RAUDPC, RaRAUDPC, and the square root of the latter) based on the distributions of cultivar rankings across locations, which were evaluated numerically and graphically. Eight cultivars were compared in 13 to 15 locations (depending on cultivar) for variation among locations, which was indicated by the coefficient of variation (CV), based on the variance among locations, using each of the variables mentioned above.

The second step in the analysis strategy involved evaluation of different approaches to assigning resistance scale values to a particular disease measure (e.g., RaRAUDPC). Linear regressions were made using assigned disease classifications as the dependent variable and a disease measure as the independent variable using the general regression equation $Y = a + b_1x_1 + e$, where, Y = the dependent variable, in this case a scale value, a = the intercept, b_1 = the slope parameter, x_1 = the independent variable, and e = the error term.

Regressions were done with increasing susceptibility (i.e., 1 was resistant and higher numbers indicated increasing susceptibility). In some regressions, only one reference cultivar was used. For these, the scale value of Bintje was assigned to 8 based on its high level of susceptibility (1,18). In other regressions, Cruza 148 was added as a second reference cultivar, with a level of 1.81, which had been derived from the regression using only Bintje. When only one reference cultivar was used, the regression line was forced through the origin ($a = 0$ in the model), but this was

not done when two reference cultivars were used. A regression was run for each location–year combination, using only the mean RaAUDPC of Bintje, or of Bintje and Cruza 148, and the assigned values described above for one or both of the two cultivars. Scale values for the remaining cultivars for each location–year combination were then estimated using each cultivar’s RaAUDPC value and the estimated regression parameters ($x = 0$ and b_1 for the one-cultivar model and x and b_1 for the two-cultivar model). These estimated scale values were examined graphically and numerically. Variances of the one-reference cultivar and two-reference cultivar measures were compared using a paired t test as described by Bland and Altman (3). Prior to performing the t test, variances were log transformed to correct for dependency between variance and mean.

RESULTS

Choice of disease metric. Based on the CVs of the disease measures, there was a clear reduction in variation among locations as more complex disease measures were used (Table 1). There was a slight improvement in CVs when the AUDPC was standardized to the RAUDPC, and a notably greater improvement when RaAUDPC was used. The CV also continued to descend by using the square root of RaAUDPC but this reflects an artifact of increasing means, which results from taking square roots of the decimal RaAUDPC values. Based on paired t tests, all reductions in CV value were statistically significant at $P = 0.05$, except for the reduction going from RaAUDPC to the square root of this variable. Because of its reduced variability and relative interpretability, the RaAUDPC was chosen as the independent variable in the regression analyses.

Conversion of disease measures to resistance scale values. Both one-reference cultivar and two-reference cultivar models gave similar scale values for cultivars and, in both cases, Cruza-148 and Bintje were the most resistant and most susceptible

genotypes, respectively (Table 2). CVs of estimated scale values were consistently, if only slightly, smaller for the two-cultivar model. This difference was significant based on a paired t test of variances of the two measures ($t = -4.23$, $P = 0.0039$).

DISCUSSION

In this article, we have evaluated some of the factors affecting the estimation of scale values for potato genotypes with different levels of susceptibility to *P. infestans*. Based on our analyses, it appears that a simple and effective scale can be developed using one of several commonly used or easily calculated measures of disease severity; for example, the AUDPC or the RAUDPC. However, there are a number of issues that needed to be considered, including the nature of the scale, the disease measure to use, the regression model, and the “conceptual focus” of the scale (i.e., resistance or susceptibility). There are also several assumptions that apply to any attempt to compare genotypes across experiments.

Nature of scale. As noted previously, only interval or ratio scales are appropriate for most mathematical or statistical manipulations. If a scale is developed from simple regression on the AUDPC, RAUDPC, or RaAUDPC, then the scale should be at least an interval type or, potentially, ratio (discussed later). The scale value in these cases is a direct function of the disease measure and both metrics would have similar properties in the scheme of Stevens (16). Statistical analyses using the AUDPC or the RAUDPC as response variable are abundant in the literature (13). A regression approach based on one of these disease measures would result in scale values that are similarly appropriate for statistical analyses. This is less clear with the approach taken by Hansen et al. (11), in which the independent variable is a square root transformation of the RaAUDPC.

Which disease measure? For a one-reference model with ascending values corresponding to increasing susceptibility, AUDPC, RAUDPC, and RaAUDPC give identical results (data

TABLE 1. Comparison of different measures of disease severity used to evaluate susceptibility in eight potato genotypes grown in trials in Europe and North America^a

Cultivar	AUDPC		RAUDPC		RaAUDPC		Square root of RaAUDPC	
	Mean	CV	Mean	CV	Mean	CV	Mean	CV
Alpha	986	0.52	0.30	0.47	0.78	0.19	0.88	0.10
Bintje	1,255	0.43	0.41	0.41	1	0.00	1	0.01
Cruza 148	258	0.56	0.08	0.50	0.21	0.48	0.43	0.28
Eigenheimer	1,077	0.54	0.35	0.51	0.82	0.20	0.90	0.10
Record	878	0.55	0.28	0.50	0.67	0.19	0.81	0.10
Robijn	603	0.78	0.19	0.79	0.42	0.45	0.64	0.20
Seseni	583	0.74	0.18	0.61	0.41	0.39	0.62	0.19
Yungay	614	0.76	0.19	0.58	0.44	0.45	0.64	0.27

^a Values presented are means and standard deviations (across trials) calculated from the trial mean value of area under the disease progress curve (AUDPC), relative AUDPC (RAUDPC), the RAUDPC divided by the RAUDPC of Bintje (RaAUDPC), and the square root of the RaAUDPC from each of the trials. CV = coefficient of variation, which is the standard deviation expressed as a proportion of the mean.

TABLE 2. Estimated susceptibility scale values for potato cultivars derived from regression analyses involving one reference cultivar (Bintje) or two reference cultivars (Bintje and Cruza-148) using the relative area under the disease progress curve (RAUDPC) as the independent variable

Cultivar	One reference cultivar ^a			Two reference cultivars ^b		
	Trials	Scale value	CV ^c	Trials	Scale value	CV ^c
Bintje	15	7.79	0.05	14	7.76	0.05
Eigenheimer	13	6.18	0.20	12	6.34	0.16
Alpha	13	6.14	0.17	12	6.10	0.15
Record	13	5.04	0.20	12	5.29	0.15
Yungay	15	3.31	0.48	14	3.77	0.31
Robijn	15	3.29	0.44	14	3.62	0.37
Seseni	15	3.18	0.39	14	3.54	0.31
Cruza-148	14	1.59	0.48	14	2.05	0.20

^a The single reference cultivar was Bintje and it was given an assigned scale value of 8.
^b In this case, Bintje (scale value = 8) and Cruza-148 (scale value = 1.81) were used.
^c CV = coefficient of variation, which is the standard deviation expressed as a proportion of mean.

not shown). With any disease measure, the slope of the line predicting susceptibility scale values from the disease measure is equal to S_y/D_y , where S_y and D_y represent the susceptibility scale value and observed disease measure (such as AUDPC) for the standard genotype, respectively (Fig. 1). The predicted susceptibility S_x of another cultivar would be calculated from this slope and the observed disease D_x and, thus, $S_x = (S_y/D_y)D_x$ or $S_x = S_y(D_x/D_y)$.

Thus, the predicted susceptibility scale value of any candidate genotype is the scale value of the standard cultivar multiplied by the observed disease measure of the candidate genotype divided by the disease measure of the standard genotype. Thus, any transformation of the disease measure by dividing or multiplying by a constant will not change the predicted susceptibility class. For example, if the initial disease measure is the AUDPC and one transforms this by calculating the RAUDPC (by dividing by the maximum AUDPC from the duration of the epidemic), this division affects both D_x and D_y equally and the resulting susceptibility scale values will not be changed. In a similar manner, using the RaAUDPC will not change the susceptibility scale values.

The relationship between the observed disease measure and the susceptibility scale may not always be linear. This is a characteristic that can be manipulated by transformation. If one is interested in having greater resolution at the more resistant end of the scale, one could use a logarithmic transformation of the disease measure. This is similar to the approach taken by Hansen et al. (11), where the square root transformation of RaAUDPC would give increased resolution at the resistant end of the scale (note that, for the Hansen et al. [11], scale values were reversed). On the other hand, if greater resolution is needed on the susceptible end of the scale, then a transformation involving squaring or exponentiating would be more useful. However, as noted above, transformations such as these may affect the appropriateness of the scale measure for statistical analyses and would reduce their intuitive interpretability.

Regression models. Regression models of both 1 and 2 reference genotypes gave relatively similar results, indicating that, for the sake of simplicity, one genotype will probably work. Having two reference genotypes may provide security against hazards that may affect the viability or validity of one of them; as, for example, if one genotype is not well adapted or severely affected by other biotic constraints. However, using only one resistant reference genotype is probably not advisable because all of the

Fig. 1. Graphical derivation of scale values for susceptibility of potato genotypes to *Phytophthora infestans* based on a single reference genotype. The slope of the calibration line is S_y/D_y , where S_y and D_y represent the susceptibility scale value and observed disease measure of the reference genotype, respectively, and the predicted value for a test genotype with disease level D_x would be $S_y(D_x/D_y)$, where D_x is the observed disease measure of that genotype.

calculated scale values would be an extrapolation of the regression line estimated by the resistant genotype and the origin. Therefore, in practice, it may be advisable to have additional replicates of the susceptible reference genotype.

Conceptual focus. In our regression analyses, we used a scale where ascending numbers represent increasing susceptibility. An inverse scale has been in use for many years and is similar to the method whereby the European Potato Association (available online) classifies resistance to *P. infestans* in potato. However, the use of a different term (susceptibility versus resistance) avoids possible confusion, and we have presented a number of arguments for using a scale where ascending numbers represent increasing susceptibility. The most appealing reason is that any measure of disease will increase with increasing susceptibility and, thus, the

Fig. 2. Estimated susceptibility scale values (based on area under the disease progress curve or relative area under the disease progress curve relative to Bintje) for potato cultivars with differing levels of susceptibility to *Phytophthora infestans*. Data represent locations from three trial series described in Forbes et al. (9). Locations include Canada (A), Denmark (B), France-Lerheu (C), France-Ploudaniel (D), The Netherlands (E), Scotland (F), and United States-Cornell (G).

susceptibility scale would be a simple transformation of the disease measure. Another related advantage is that zero disease development represents the highest level of resistance theoretically and in practice, whereas susceptibility is more open-ended, at least theoretically. Thus, the regression line developed from an ascending-susceptibility analysis would pass through the origin, where zero disease represents the highest level of resistance. If the reference genotypes are chosen carefully, the most susceptible cultivars can receive a measure of ≈ 9 . If material that is even more susceptible should appear, however, it would merely be higher than the previous maximum and, unlike the inverse scale, there would be no problems with negative numbers or truncated scales. Finally, with a zero origin for maximum resistance, the susceptibility scale would be a ratio scale, as defined by Stevens (16). All statistical measures are applicable to ratio scales, including calculation of logarithms.

If one uses a disease metric to measure susceptibility, then the absence of disease can be interpreted as the highest level of resistance. Thus, one can argue that the line representing susceptibility as a function of RaRAUDPC should pass through the origin, because that is the one point that is known. The analyses presented here show little difference between forcing the line through the origin with only one reference cultivar and using two reference cultivars. It should be remembered, however, that the selection of 1.81 for the susceptibility rating of Cruza-148 was based on regressions that passed through the origin with Bintje given the value 8.

Assumptions. With any scale, there is an important underlying assumption that resistance in cultivars is stable across experiments. In our analyses, some cultivars appear as outliers when scale values are examined across experiments (Fig. 2). This is due to variability in the results caused by uncontrolled factors and this cannot be corrected by a scale. Many sources of variation that may lead to experiment by cultivar interactions can be envisioned, including host-pathogen interactions, poor cultivar adaptation in some locations, and even human error. A simple scale which may eliminate some sources of variation can help researchers develop hypotheses about others, and results we present here (Fig. 2) demonstrate that.

Utilization of a susceptibility scale. The AUDPC has been used as a single measure to quantify the amount of disease in an epidemic. As such, it combines information about all aspects of the epidemic, including inoculum, environment, and host susceptibility. Thus, if it is to be used to represent susceptibility alone, some simple method is needed to eliminate the variation from the other disturbing factors. The use of RAUDPC is one way in which this normalization can be done (10). In our analyses, RAUDPC of the same cultivar varied among trials and, thus, it was of limited use in quantifying susceptibility. The effect of initial inoculum on RAUDPC was pointed out by Fry (10). One note of caution: references to AUDPC in the article by Fry (10) would be called RAUDPC using the terminology herein.

Location-specific variations in the rate of disease development (from different environmental conditions or different genotypes of *P. infestans*) could also affect RAUDPC. The calculation of RaRAUDPC is one way to correct for this variation. Thus, in technical terms, the RaRAUDPC is an alternative disease measure that could be used for classifying potato genotypes for susceptibility to *P. infestans*. However, the simpler 1-to-9 scale gives numbers that are easier to remember and interpret. When one considers the large number of traits a plant breeder must consider, it is easy to understand why simple scales of this type have been preferred.

In the utilization of a scale (or the RaRAUDPC, for that matter), one or more reference genotypes must be selected. We chose Bintje as a susceptible cultivar because it has been long known for its susceptibility, which has been demonstrated in recent articles (1,18). The utility of this type of scale would be enhanced if a common reference genotype is utilized throughout a region (for example, the highland tropics).

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