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The use of the area under the disease-progress curve (AUDPC) to assess quantitative disease resistance in crop cultivars

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Abstract Calculation of the area under the disease-progress curve (AUDPC) as a measure of quantitative disease resistance entails repeated disease assessments. For typical sigmoid disease-progress curves, repeated assessments may be unnecessary. A mathematical procedure is derived for estimating the AUDPC from two data points. A field trial with ten cultivars with and without the gene *Yr18* for resistance to stripe rust were inoculated with two pathotypes of *Puccinia striiformis* (from the cultivars Karamu and Oroua) and assessed for the percentage leaf area infected seven or eight times during the growing season. The AUDPCs were calculated directly from data and estimated from the described equation. Calculated values were plotted and ranked against estimated values, and excellent correspondence was obtained (Spearman's Rank Correlation in the Karamu trial= 0.9879 and the Oroua trial=0.9515). Therefore, an estimation of the AUDPC from two data points provides an equivalent amount of information as from repeated assessments.

Keywords Disease assessment · Quantitative resistance · *Puccinia striiformis* f.sp. *tritici* · Wheat · area under the disease-progress curve

Introduction

Plant-disease epidemiologists have long been interested in the temporal increase of disease as characterised by a disease-progress curve. Simple descriptive growth models have often served to characterize the overall patterns of disease increase in time (Pennypacker et al. 1980; Berger 1981; Luke and Berger 1982; Thal et al. 1984; Subba Rao et al. 1990) or in time and space (Berger and Luke 1979; Jeger 1983; Headrick and Pataky 1988; Damicone et al. 1990). In some cases epidemiologists have used these models to estimate rate parameter, or other disease-progress parameters that may be of use in identifying cultivars that express different patterns of disease progress in the field (MacKenzie 1976) or how these patterns may be influenced by different components of partial resistance (Das et al. 1993; Aquino et al. 1995). Leonard and Mundt (1984) related the rate of disease progress to changes in the components of quantitative resistance, but during the exponential phase of an epidemic only.

In at least two areas, those of crop-loss assessment (Ferrandino and Elmer 1992) and field assessment of partial or quantitative resistance, the use of disease-progress data has been developed further through the calculation of the area under the disease-progress curve (AUDPC). This measure has been used to average out the undoubted variation and idiosyncrasies (Royle 1994) often seen in disease-progress curves, and also to integrate all aspects of disease progress in relation to host development and growth. Most applications have been made in field assessment of high levels of resistance. Techniques for calculating the AUDPC are based on simple formulae (Wilcoxson et al. 1975; Shaner and Finney 1977; Bjarko and Line 1988; Das et al. 1992: Chen and Line 1995; Miedaner and Sperling 1995; Broers et al. 1996) such as the trapezoidal rule for calculating areas. In a different context, the area under the linear-regression function of genotype yield against an index of environmental productivity has been proposed as a selection criterion in plant breeding (Hernandez et al. 1993).

A representative range of publications concerned with the assessment of quantitative resistance using AUDPC is summarized in Table 1. These publications all deal with foliar fungal pathogens on annual crops, where

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Table 1 Selected publications in which use of the AUDPC in breeding for disease resistance was reported

Host and pathogen	Method of comparison	Sampling method, unit	Assessments, interval, start times and finish times	Formulae for the AUDPC	Disease severity data present?	Reference
Wheat – *Erysiphe graminis* f.sp. *tritici*	Field experiment over 4 years with two cultivars in four-row plots (2.4 m), nitrogen and cultivar treatments arranged in a split-plot design	Mildew severity (% leaf area covered) assessed for each of the upper four leaves for five plants per plot	Five or six times at 7-day intervals starting end of April – early May and finishing early June	$\sum_{i=1}^{n}[(Y_{i+n1}+Y_i)/2][X_{i+1}-X_i]$ Y_i=mildew severity (per unit) at the *i*th observation, X_i=time (days) at the *i*th observation *n*=total number of observations	Yes	Shaner and Finney (1977)
Wheat – *Puccinia graminis* f.sp. *tritici*	Field experiments over 3 years at several locations planted in hill plots (15 seeds per hill) with ten replications. Plots were inoculated with a single pathotype or mixtures of pathotypes	Severity assessed on each hill using a modified Cobb scale	Four times at 7-day intervals	$\sum_{i=1}^{k}\frac{1}{2}(s_i+s_{i-1})$ s_i=rust severity at the end of week *i* *k*=number of successive evaluations of rust	No	Wilcoxson et al. (1975)
Wheat – *Puccinia recondita* f.sp. *tritici*	Two field experiments were carried out with six spring wheat cultivars crossed in a diallel series, parents and progenies to the F_6. There were three replicates and 30 seeds per line in 1.5 m-long rows	Severity (average value and reaction type) assessed on ten flag leaves in the middle of each plot	Three times at 7-day intervals; first time 11-days after inoculation	$\sum_{i=1}^{n-1}[(x_i+x_{i+1})/2](t_{i+1}-t_i$ x_i=leaf rust severity on the *i*th date, t_i=*i*th day, n=number of dates on which disease was recorded	Some	Das et al. (1992)
Wheat – *Puccinia recondita* f.sp. *tritici*	Field experiment with 26 cultivars, three replicates, and two 1-m-rows per plot	Severity and infection type recorded on flag leaves	Three times at 10-day intervals (from first symptoms to late flowering stage)	CIMMYT (not expressed)	No	Singh (1993)
Wheat (synthetic hexaploid) – *Puccinia striiformis* f.sp. *tritici*	Field experiment with 34 lines of *T. turgidum* and 267 synthetic hexaploid wheats; two sites and two replicates	Severity assessed for each plot	Three times at 10-day intervals starting when the susceptible cultivar had reached 100% severity	CIMMYT, expressed as relative AUDPC (percentage of the susceptible check)	No	Ma et al. (1995)
Wheat –*Puccinia striiformis* f.sp. *tritici*	Ten bread wheat cultivars were planted in three field sites, sites 1 and 2 had two experiments each with three replicates per site, site 3 had four replicates in one experiment	Site 1: severity on the upper two leaves of 15 tillers Site 2: severity on the upper two leaves of ten tillers Site 3: as in site 1 Average disease severity for each plot was transformed to logits and regressed against time	Site 1: Four times at 7-day intervals Site 2: Five (Experiment 1) or six (Experiment 2) times at 5–8 day intervals Site 3: Nine times at 4-day intervals	$\sum_{i=1}^{n}[t(i+1)-t_i]\times[DS(i+1)+DS_i]/2$ *n*=number of assessments, t_i=number of days after inoculation on assessment date *i*, DS_i=disease severity on assessment date *i*	Some	Broers et al. (1996)

Table 1 continued

Host and pathogen	Method of comparison	Sampling method, unit	Assessments, interval, start times and finish times	Formulae for the AUDPC	Disease severity data present?	Reference
Wheat – *Puccinia recondita* f.sp. *tritici*	Seed from six wheat cultivars was planted in a glasshouse and reciprocal crosses were made in all combinations. Individual seeds of the parental, F_1, F_2, and backcross populations were planted in the field in five randomised blocks	Rust intensity on individual plants was measured; the scale of the data was changed using an arcsin transformation	Six times (11, 17, 24, 31 July and 7 and 8 August)	$\sum_{i=1-5}[(x_i + x_{i+1})/2]t_i$ x_i=the transformed rust intensity on date i t_i=time in days between date i and date i+1	Yes	Bjarko and Line (1988)
Wheat – *Blumeria graminis* f. sp. *tritici*	One susceptible and six adult plant-resistant winter wheats were crossed and seeds of parents, F_1 and F_2 populations were sown in the field during two seasons. There were three replicates in a randomised complete block design	Severity was assessed on the penultimate leaves of five vigorous plants in the first year; in the 2nd year, several penultimate leaves of each plant were evaluated and given an average mildew severity value per plant	Three times at 7-day intervals	Formula of Bjarko and Line (1988)	No	Das and Griffey (1994)
Wheat – *Stagonospora nodorum*	Two glasshouse experiments. The first included 13 cultivars and lines in a randomised complete-block design with five replications. The second experiment consisted of crosses between two lines (3800 plants)	Severity assessed on spikes and flag leaves	Experiment 1: seven assessments, 5, 7, 11, 13, 15, 18, 20 days after inoculation Experiment 2: seven assessments 6, 7, 9, 10, 15, 16, 20 days after inoculation	Formula of Shaner and Finney (1977)	No	Bostwick et al. (1993)
Potato – *Phytophthora infestans*	Field experiment with 16 cultivars, three replicates	Severity assessed on 40 (of 72) plants per plot	Six assessments at 10-day intervals	Formula of Shaner and Finney (1977)	No	Birhman and Singh (1995)
Tomato – *Pseudocerospora fuligena*	A total of 620 accessions of wild *Lycopersicon* or their crosses with *L. esculentum* were carried out in glasshouse. Twenty of those were selected for field and growth-room experiments	Growth room: six seedlings per accession, three replicates, percentage leaf area infected Field: four replicates of one plant, percentage of leaf area infected	Growth room: seven assessments at 2-day intervals. Field: nine assessments at 7-day intervals	Formula of Shaner and Finney (1977)	Some	Hartman and Wang (1993)
Cowpea – *Erysiphe graminis*	Glasshouse experiment with 20 germplasm lines, five replicates	Mildew severity and incidence on each leaf	Four times at 3–4-day intervals	Formula of Wilcoxson et al. (1975)	Yes	Raju and Anilkumar (1990)

Table 1 continued

Host and pathogen	Method of comparison	Sampling method, unit	Assessments, interval, start times and finish times	Formulae for the AUDPC	Disease severity data present?	Reference
Wheat – *Puccinia recondita* f.sp. *tritici*	Two field experiments, first with one cultivar studying the effect of the time of inoculation on disease development, and the second with three cultivars to study spatio-temporal spread	I: three replicates, severity on ten tillers assessed II: three replicates, severity on five tillers around the point source and at each sampling distance in four directions; also temperature, leaf wetness and yield assessed	I: up to 12 times at 7-day intervals from first signs to senescence II: ten times at 7-day intervals	Formula of Shaner and Finney (1977)	Some	Subba Rao et al. (1990)
Wheat – *Puccinia graminis* f.sp. *tritici* and *Puccinia recondita* f.sp. *tritici*	Two field experiments in consecutive years; two 0.4-ha plots per experiment	Stem and leaf rust uredinia counted on all culms and on the living flag and penultimate leaves. Stem rust severity assessed on the peduncle and on the flag leaf sheat	Severity was measured six times at 7-day intervals	Formula of Shaner and Finney (1977)	Some	McGrath and Pennypacker (1991)
Wheat – *Puccinia striiformis* f.sp. *tritici*	One field experiment to assess disease severity on several parents and progeny of crosses to the F_2 population	Infection types and severity measured for plots	Two or three times	$\sum[(x_i + x_{i+1})/2](t_{i+1} - t_i)$ x_i=the rust intensity of the *i*th note, x_{i+1}=rust intensity of the *i+1*th note, $(t_{i+1} - t_i)$=the number of days between the *i*th note and the *i+1*th note	No	Chen and Line (1995)
Maize – *Cercospora zeae-maydis*	Two field experiments of seven (two replicates) or 19 (three replicates) inbred lines	Disease severity and disease-index score assessed in each of 12 plants per plot	Nine times over 35 days or ten times every 5 days	Formula of Shaner and Finney (1977)	Some	Saghai Maroof et al. (1993)
Winter rye – *Puccinia recondita* f.sp. *secalis*	Three field experiments of ten single crosses, three replicates	Mean leaf rust rating given separately on the upper three leaves in ten tillers per plot	Four assessments but only some used in different sites	$\sum_{i=1}^{n}[(x_i + x_{i-1}) \times 0.5] \times t_1$ *n*=total number of assessment dates, x_i=leaf rust rating at the *i*th assessment date, t_i=time in days between date *i*and date *i*-1	No	Miedaner and Sperling (1995)

there are many cycles of pathogen multiplication within a growing season. They cover a range of assessment methods and sampling frequencies (up to 12 assessment dates per growing season). In some cases data were presented graphically, or comments were made on the shape of the disease-progress curve; many were, or were considered to be, of a sigmoid or logistic shape.

The purpose of our investigation was to determine whether, for sigmoid curves at least, the amount of sampling and the number of assessments made was actually necessary to estimate the AUDPC. In cases where a well-defined period for assessment exists (i.e. in terms of growth stages), then as few as two assessments are sufficient to provide most of the information present in calculations of the AUDPC. We do this by analysing the properties of sigmoid curves, notably the logistic growth function, and by reference to data on stripe rust epidemics on a number of different wheat cultivars.

Mathematical procedures

For any real, continuous function $y=f(t)$ (with $y>0$) the area under the function is simply the definite integral evaluated between the limit of integration t_0 and T, where $T>t_0$.
Suppose

$$y = f(t) = \frac{1}{1+Ae^{-rt}} \qquad (1)$$

with $A=(1-y_0)/y_0$, where y_0 is the value of y at $t_0=0$, and r is a rate parameter. Conventionally we set $t_0=0$ to correspond to the earliest date that disease is observed in a crop, and thus to the start of an epidemic. Equation 1 is the well-known logistic function with y restricted to the values 0–1, and has often been used to describe disease-progress curves where disease incidence or severity is measured as a proportion. The area under a disease-progress curve described by equation 1 is then

$$AUDPC = \int \frac{dt}{1+Ae^{-rt}}$$

which, evaluated between the limits $t=0$ and T, and substituting in y,

$$= T + \frac{\ln\left(\frac{y_0}{y_T}\right)}{r} \qquad (2)$$

where y_T is the value of $f(t)$ at $t=T$. We interpret T as the time of harvest, or time of some preceding critical growth stage. It should be noted that as T increases, y_T approaches the value 1 and equation 3 is simply a linear equation in T.

If we have values for y_0 and y_T and have estimates of the rate parameter r then the AUDPC follows immediately from equation 2. An estimate of the rate is obtained from the formula:

$$r = \frac{\ln\left(\frac{y_T}{1-y_T}\right) - \ln\left(\frac{y_0}{1-y_0}\right)}{T}. \qquad (3)$$

Thus, only two assessments of disease are necessary, one at the start of an epidemic and one at the end or at a critical growth stage. Equation 3 can actually be inserted directly into equation 2 to obtain a single expression for the AUDPC.

Materials and methods

Two autumn-sown field experiments were established (sowing date 23 May 1996) at Lincoln, New Zealand (latitude 43°38′S, longitude 152°20′E, altitude 11 m), to determine stripe rust severity (caused by *Puccinia striiformis* Westend. f.sp. *tritici*) on 16 wheat cultivars with and without the *Yr18* gene for resistance (data for ten cultivars are presented in this paper). The spreader rows of either of the wheat cultivars, Karamu or Oroua, were inoculated with the pathotype 106E139A+ (isolated from Karamu) or 106E139A– (isolated from Oroua), respectively. Both pathotypes were virulent on the genes *Yr*2 and *Yr*7 present in some of the test cultivars (Viljanen-Rollinson and Cromey 1998). Each experiment was conducted in a completely randomised block design with four replicates. Each replicate consisted of 16 plots. Each plot consisted of six 1.2-m drill rows; the first, third, fourth and sixth rows were sown with spreaders (Karamu or Oroua) while the second and fifth rows were the respective test cultivars. The spreader rows were inoculated (Cromey 1992) by planting 40 pots of glasshouse-grown plants of the cultivar Tiritea infected with either pathotype 106E139A+ (Karamu trial) or 106E139A– (Oroua trial) when the plants at the experimental site had one fully emerged leaf. Disease was scored on seven (Oroua trial) or eight (Karamu trial) occasions giving each cultivar a score (percentage of leaf area infected) based on the modified Cobb's scale for measuring rust severity (Peterson et al. 1948), derived from the whole row.

Results

Disease-progress curves for the ten cultivars (means over replicates) are shown in Fig. 1 using the *P. striiformis* pathotype derived from the cultivars Karamu and Oroua. Data were transformed to logits and estimates of slope and initial disease (y_0) were obtained for each cultivar by linear regression (Table 2). In all cases statistically significant fits were of $P=0.05$ or greater significance, with coefficients of determination (R^2) ranging from 0.40 to 0.99 with the Oroua pathotype, and 0.66 to 0.96 with the Karamu pathotype.

The AUDPCs were calculated numerically using the trapezoidal rule and are plotted for successive assessment dates in Fig. 2. The AUDPC values calculated directly from the data for all assessments up until day 67, and those estimated from equation 2 based only on assessed values on days 14 and 67 (Table 3), generally show a good correspondence (Spearman's Rank Correlation in the Karamu pathotype=0.9879 and in the Oroua pathotype=0.9515).

A more-thorough procedure for checking the correspondence between the calculated and estimated AUDPC is to estimate a matching value for each of the cumulative AUDPCs in Fig. 2 and plot the estimated (based on two assessments) against the actual calculated values. This was done for each of the ten cultivars across both pathotype sources (Karamu and Oroua) and for

each pathotype source across all cultivars (Fig. 3). The estimated slopes for the cultivars ranged from 0.83 to 1.85 with R^2 values ranging from 0.77 (Avocet R) to greater than 0.92 (all other cultivars). Figure 3A shows the calculated values plotted against the estimated values for trials with the Karamu pathotype across all cultivars. Although, as would be expected, values coincide at lower AUDPCs there is little divergence between values of about 10 and 30. The slope of the fitted line was 1.12 (SE=0.04) with an R^2 value of 0.92. Figure 3B shows calculated values plotted against estimated values for trials with the Oroua pathotype across all cultivars. By contrast with Karamu, there was divergence in values above AUDPCs of about 15. The slope of the fitted line was 1.02 (SE=0.05) with an R^2 value of 0.86.

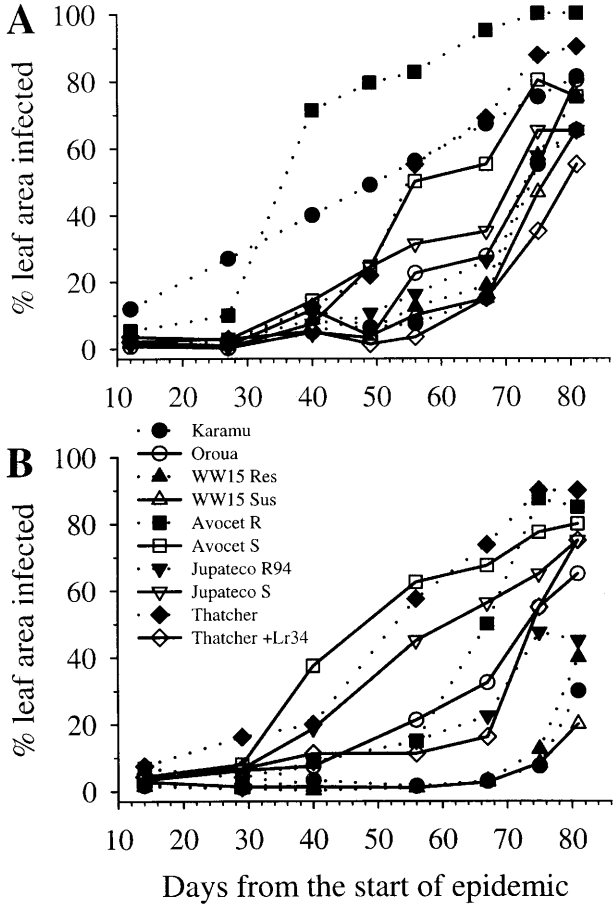

Fig. 1 **A** Disease severity of stripe rust on ten wheat cultivars assessed on eight occasions (intervals of 12–14 days for the first three assessments, 6–9 days for the last five assessments; Day 0=3 Oct 1996) using pathotype 106E139A$^+$ derived from cultivar Karamu. **B** Disease severity of stripe rust on ten wheat cultivars assessed on seven occasions (intervals of 11–16 days for first five assessments, 6–8 days for last two assessments; day 0=3 Oct 1996) using pathotype 106E139A$^-$ derived from the cultivar Oroua

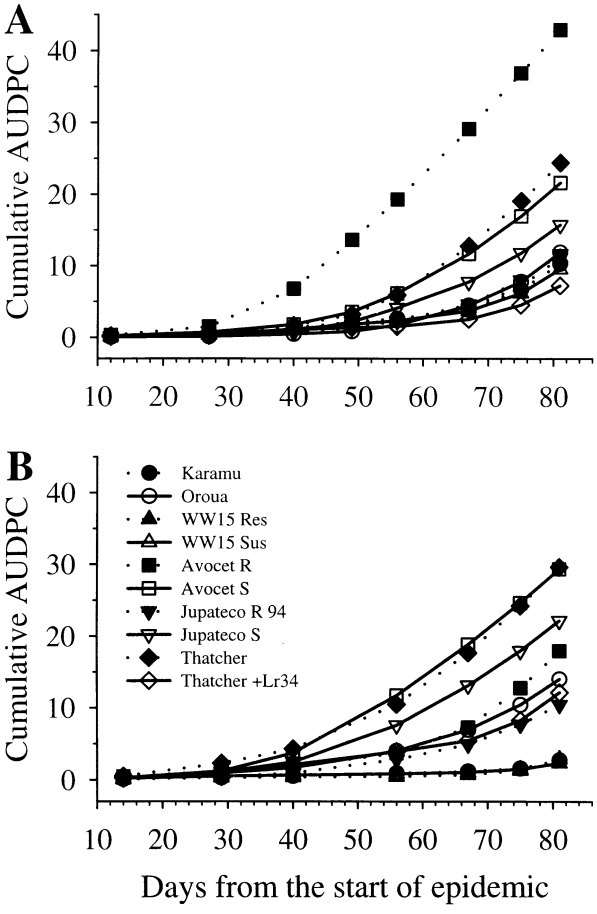

Fig. 2 The cumulative AUDPC of stripe rust on ten wheat cultivars inoculated with the pathotype derived from **A** the cultivar Karamu and **B** the cultivar Oroua (values calculated from data presented in Fig. 1)

Table 2 Linear regression of logit-transformed disease data (Fig. 1) against time for ten wheat cultivars inoculated with two pathotypes of *P. striiformis* f.sp. *tritici* (standard error in parenthesis)

Cultivar	Karamu pathotype			Oroua pathotype		
	logit Y_0	R	R^2	logit Y_0	R	R^2
Karamu	–5.18 (0.800)	0.063 (0.013)	0.80	–5.25 (0.925)	0.038 (0.015)	0.56
Oroua	–7.29 (0.932)	0.100 (0.015)	0.88	–4.50 (0.305)	0.060 (0.005)	0.97
WW15 R	–5.55 (0.668)	0.072 (0.011)	0.89	–6.54 (1.410)	0.056 (0.023)	0.54
WW15 S	–5.59 (0.842)	0.067 (0.013)	0.81	–4.98 (0.989)	0.030 (0.016)	0.40
Avocet R	–4.46 (0.563)	0.114 (0.009)	0.96	–4.86 (0.969)	0.077 (0.016)	0.82
Avocet S	–4.77 (0.521)	0.076 (0.008)	0.93	–3.92 (0.469)	0.070 (0.008)	0.94
Jupateco R	–5.89 (0.445)	0.076 (0.007)	0.95	–5.28 (0.659)	0.064 (0.011)	0.87
Jupateco S	–6.10 (0.798)	0.087 (0.013)	0.89	–4.20 (0.222)	0.066 (0.004)	0.99
Thatcher	–5.28 (0.607)	0.092 (0.010)	0.94	–3.87 (0.338)	0.075 (0.006)	0.97
Thatcher +*Lr34*	–5.27 (1.020)	0.055 (0.016)	0.66	–4.27 (0.775)	0.054 (0.013)	0.79

Table 3 Comparison of the calculated (directly from the data for all assessments until day 67) and estimated (from equation 2 based only on assessed values on days 14 and 67) AUDPC of stripe rust on ten cultivars inoculated with two pathotypes of *P. striiformis* f.sp. *tritici*, after 67 days

Cultivar	Karamu pathotype		Oroua pathotype	
	Calculated	Estimated	Calculated	Estimated
Karamu	3.88	3.84	1.19	1.23
Oroua	4.48	4.41	6.97	7.25
WW15 R	4.11	3.99	0.71	1.15
WW15 S	3.70	3.53	1.07	1.46
Avocet R	28.98	27.93	7.31	12.65
Avocet S	11.66	11.00	18.89	14.99
Jupateco R	4.61	4.93	4.92	4.93
Jupateco S	7.75	6.13	13.16	12.15
Thatcher	12.71	15.34	17.72	18.83
Thatcher +*Lr34*	2.53	3.70	5.44	4.86

Finally the rankings of cultivars with respect to calculated and estimated rates of disease progress and the AUDPC are summarized in Table 4. For the rate parameters there was some discrepancy in rankings for some cultivars, especially with the Oroua pathotype (Spearman's Rank Correlation in the Karamu pathotype=0.9636 and in the Oroua pathotype=0.8303). For the AUDPC there was excellent correspondence between rankings based on calculated and estimated values (Spearman's Rank Correlation in the Karamu pathotype=0.9879 and in the Oroua pathotype=0.9515).

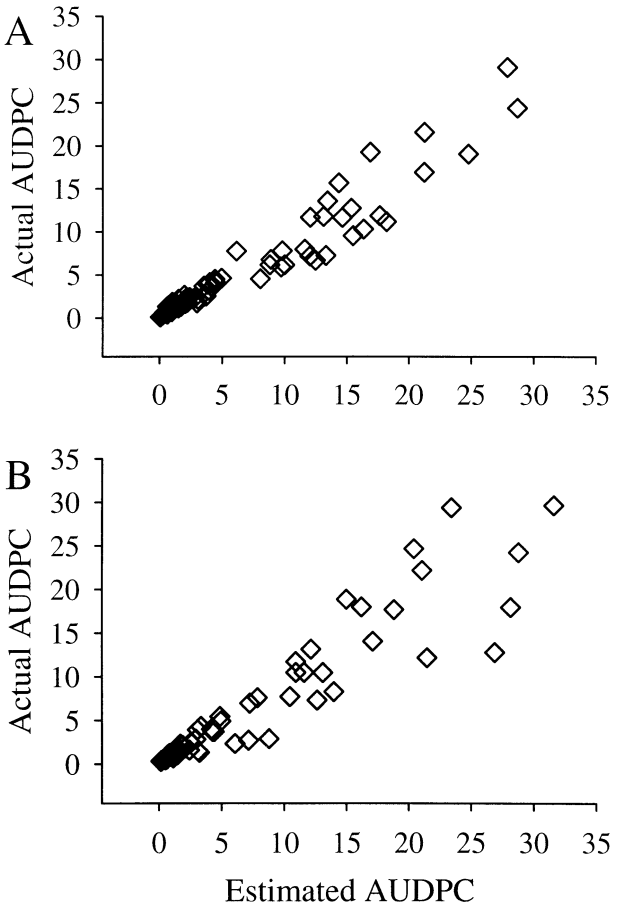

Fig 3 Correspondence between the calculated and estimated (equation 2) AUDPC of stripe rust on ten wheat cultivars inoculated with pathotypes derived from Karamu and Oroua: combined data across all cultivars for the pathotype derived from cultivar-**A** Karamu and -**B** Oroua

Conclusions

Disease assessment represents a considerable investment in time, space, and human resources. There are limitations on how frequently assessments can be made, especially in small-plot trials involving large numbers of cultivars or breeding lines. The use of the calculated AUDPC has increased in recent years and can certainly be recommended when, because of either host phenology or growth, monotonically increasing disease progress is unlikely. Particularly for polycyclic foliar pathogens, however, where resistance is expressed quantitatively, the estimation technique introduced in this paper, based on as few as two assessments, may provide as much information as repeated sequential assessments. Three qualifications should however be made. Firstly, the effect of resistance should be expressed in terms of the rate parameter ('rate-reducing' resistance) and not the asymptotic level of disease – a complication that may arise, for example, with adult plant resistance. This assumption was reasonable for the particular trial data analysed in this paper, but may not always be the case. Secondly, in the trial data the period of time over which disease was present in the crop was the same for each of the ten cultivars. This might not always be the case and would need to be accounted for in the estimation procedure. Thirdly, where infection is not continuous but dependent upon discrete environmental events, then sigmoid curves may not arise and the technique introduced may give anomalous results. Das et al. (1993) also suggested that using a single measurement of rust severity, measured toward the end of the epidemic, would help in selecting slow rusting genotypes, if resources were limited and several disease readings are not available to compute the AUDPC.

Many measures of disease have been advocated for use in resistance screening, including single-point assessments at key growth stages, calculating rates of disease development, and calculating areas under disease-progress curves. Recently it has been found that quantitative trait loci are associated with partial resistance to barley leaf rust, determined on the basis of the AUDPC (Qi et al. 1998). We believe that the estimation procedure we describe offers an optimisation of the information to be gained from field disease assessments, and the time and calculation effort required for making the assessments.

Table 4 Ranking of ten wheat cultivars with respect to calculated and estimated rate parameters and the AUDPC for stripe rust disease progress

Cultivar	*r*-value		AUDPC	
	Calculated (Table 2)	Estimated (67 days, equation 3)	Calculated (67 days)	Estimated (67 days, equation 2)
(**a**) Karamu trial				
Karamu	2	1	3	3
Oroua	9	8	5	5
WW15 R	4	4	4	4
WW15 S	3	3	2	1
Avocet R	10	10	10	10
Avocet S	6	6	8	8
Jupateco R	5	5	6	6
Jupateco S	7	7	7	7
Thatcher	8	9	9	9
Thatcher +*Lr34*	1	2	1	2
(**b**) Oroua trial				
Karamu	2	2	3	2
Oroua	5	7	6	6
WW15 R	4	3	1	1
WW15 S	1	1	2	3
Avocet R	10	6	7	8
Avocet S	8	10	10	9
Jupateco R	6	5	4	5
Jupateco S	7	8	8	7
Thatcher	9	9	9	10
Thatcher +*Lr34*	3	4	5	4

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References

Aquino VM, Shokes FM, Gorbet DW, Nutter FW (1995) Late leaf spot progression on peanut as affected by components of partial resistance. Plant Dis 79:74–78

Berger RD (1981) Comparison of the Gompertz and logistic equations to describe plant disease progress. Phytopathology 71:716–719

Berger RD, Luke HH (1979) Spatial and temporal spread of oat crown rust. Phytopathology 69:1199–1201

Birhman RK, Singh BP (1995) Path-coefficient analyses and genetic parameters of the components of field resistance of potatoes to late blight. Ann Appl Biol 127:353–362

Bjarko ME, Line RF (1988) Heritability and number of genes controlling leaf rust resistance in four cultivars of wheat. Phytopathology 78:457–461

Bostwick DE, Ohm HW, Shaner G (1993) Inheritance of *Septoria* glume blotch resistance in wheat. Crop Sci 33:439–443

Broers LHM, Cuesta Subias X, Lopez Atilano R.M (1996) Field assessment of quantitative resistance to yellow rust in ten spring bread wheat cultivars. Euphytica 90:9–16

Chen X, Line RF (1995) Gene action in wheat cultivars for durable, high-temperature, adult-plant resistance and interaction with race-specific, seedling resistance to *Puccinia striiformis*. Phytopathology 85:567–572

Cromey MG (1992) Adult plant resistance to stripe rust (*Puccinia striiformis*) in some New Zealand wheat cultivars. NZ J Crop Hort Sci 20:413–419

Damicone JP, Snow JP, Berggren GT (1990) Spatial and temporal spread of soybean stem canker from an inoculum point source. Phytopathology 80:571–578

Das MK, Griffey CA (1994) Diallel analysis of adult-plant resistance to powdery mildew in wheat. Crop Sci 34:948–952

Das MK, Rajaram S, Mundt CC, Kronstad WE (1992) Inheritance of slow-rusting resistance to leaf rust in wheat. Crop Sci 32:1452–1456

Das MK, Rajaram S, Kronstad WE, Mundt CC, Singh RP (1993) Associations and genetics of three components of slow rusting in leaf rust of wheat. Euphytica 68:99–109

Ferrandino FJ, Elmer WH (1992) Reduction in tomato yield due to *Septoria* leaf spot. Plant Dis 76:208–211

Hartman GL, Wang TC (1993) Resistance in *Lycopersicon* species to black leaf mold caused by *Pseudocercospora fuligena*. Euphytica 71:125–130

Headrick JM, Pataky JK (1988) Spatial and temporal development of common rust in susceptible and partially resistant sweet corn hybrids. Phytopathology 78:227–233

Hernandez CM, Crossa J, Castillo A (1993) The area under the function: an index for selecting desirable genotypes. Theor Appl Genet 87:409–415

Jeger MJ (1983) Analysing epidemics in time and space. Plant Pathol 32:5–11

Leonard KJ, Mundt CC (1984) Methods for estimating epidemiological effects of quantitative resistance to plant diseases. Theor Appl Genet 67:219–230

Luke HH, Berger RD (1982) Slow rusting in oats compared with the logistic and Gompertz models. Phytopathology 72:400–402

Ma H, Singh RP, Mujeeb-Kazi A (1995) Resistance to stripe rust in *Triticum turgidum*, *T. tauschii*, and their synthetic hexaploids. Euphytica 82:117–124

MacKenzie DR (1976) Application of two epidemiological models for the identification of slow stem rusting in wheat. Phytopathology 66:55–59

McGrath MT, Pennypacker SP (1991) Reduction in the rate and duration of grain growth in wheat due to stem rust and leaf rust. Phytopathology 81:778–787

Miedaner T, Sperling U (1995) Effect of leaf rust on yield components of winter rye hybrids and assessment of quantitative resistance. J Phytopathology 143:725–730

Pennypacker SP, Knoble HD, Antle CE, Madden LV (1980) A flexible model for studying plant disease progression. Phytopathology 70:232–235

Peterson RF, Campbell AB, Hannah AE (1948) A diagrammatic scale for estimating rust intensity on leaves and stems of cereals. Can J Res 26:496–500

Qi X, Niks RE, Stam P, Lindhout P (1998) Identification of QTLs for partial resistance to leaf rust (*Puccinia hordei*) in barley. Theor Appl Genet 96:1203–1215

Raju SG, Anilkumar TB (1990) Evaluation of cowpea genotypes for partial resistance to powdery mildew. Euphytica 50:191–195

Royle DJ (1994) Understanding and predicting epidemics: a commentary based on selected pathosystems. Plant Pathol 43:777–789

Saghai Maroof MA, Van Scoyoc SW, Yu YG, Stromberg EL (1993) Gray leaf spot disease of maize: rating methodology and inbred line evaluation. Plant Dis 77:583–587

Shaner G, Finney RE (1977) The effect of nitrogen fertilization on the expression of slow-mildewing resistance in Knox wheat. Phytopathology 67:1051–1056

Singh RP (1993) Resistance to leaf rust in 26 Mexican wheat cultivars. Crop Sci 33:633–637

Subba Rao KV, Berggren GT, Snow JP (1990) Characterization of wheat leaf rust epidemics in Louisiana. Phytopathology 80:402–410

Thal WM, Campbell CL, Madden LV (1984) Sensitivity of Weibull model parameter estimates to variation in simulated disease progression data. Phytopathology 74:1425–1430

Viljanen-Rollinson SLH, Cromey MG (1998) The effectiveness of stripe rust resistance gene *Yr18* in wheat cultivars. Proc 51st New Zealand Plant Protection Conf, August 1998, pp 71–75

Wilcoxson RD, Skovmand B, Atif AA (1975) Evaluation of wheat cultivars for the ability to retard development of stem rust. Ann Appl Biol 80:275–287