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Inheritance of resistance to late blight (*Phytophthora infestans*) in potato

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Abstract Under epiphytotic conditions for late blight in spring seasons, data were recorded on its intensity four times at 4 days intervals from the start of the disease in the field, in 114 (19 females × 6 males) progenies and their parents planted in randomized complete block design in the years 2005 and 2006. Regression and stepwise regression analysis showed that observations during the rapidly increasing phase of disease between initial and last phase of disease are more important than the observations at initial and last phase of the disease. Combining ability analysis on a sub-set of 68 progenies showed that the additive component of genetic variance was more important than the non-additive component of variance in inheritance of quantitative resistance to late blight. The per se performance of the parents does give an idea about their general combining ability (GCA). However, selection of parents based on their GCA will be very useful for breeding for quantitative resistance to late blight. Parents JX 90, JF 4841, CP 3356, CP 1358, CP 3290, JN 1197 and CP 3125 were found to have good GCA for quantitative resistance for late blight and the best six crosses for late bilght resistance based on mean performance involved parents with good combining ability only.

Keywords *Phytophthora infestans* · *Solanum tuberosum* · Late blight · Quantitative resistance · Combining ability · Parent-progeny correlation

Abbreviations

AUDPC	Area under disease progress curve
GCA	General combining ability
SCA	Specific combining ability
SCG	Second clonal generation
TCG	Third clonal generaition

Introduction

Late blight caused by the fungus *Phytophthora infestans* (Mont.) de Bary is one of the most devastating diseases of cultivated potatoes worldwide. The disease is responsible for important economic losses and high levels of fungicide use. Potato varieties have to face the increasing threat of the re-emergence of potato late blight disease due to recent changes in the population structure of the late blight fungus which have led to the

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advent of new genotypes that are more aggressive and resistant to previously effective fungicides (Fry et al. 1993). Development of late blight resistant cultivars needs greater attention for disease management. Earlier, late blight was considered the disease primarily of the temperate world. Since 1990, late blight is appearing with regularity even in sub-tropical plains due to change in disease behaviour and population structure. In Indian plains mainly complex races (1–8 virulence factors) have been appearing since 1985 in contrast to only simple races up to 1984 (Singh and Shekhawat 1999). Race-specific resistance controlled by major resistance (R) gene is not considered to be durable due to continuous change in pathogen and in India, as in many other countries, the current strategy is to focus on polygenically controlled quantitative resistance as most valuable source of resistance (Umaerus and Umaerus 1994; Singh and Shekhwat 1999). Quantitative race-non-specific resistance contributed by minor genes is more durable as this form of resistance is effective against a broad range of pathogenic strains of *Phytophthora infestans* (Haynes et al. 1998; Landeo et al. 2000b). Information on combining ability of parents for quantitative resistance for late blight can be useful for breeding late blight resistance cultivars. Present study was therefore conducted with the objectives: (1) to study the inheritance of quantitative resistance to late blight, (2) to identify good parents contributing quantitative resistance to late blight.

Materials and methods

Plant materials

Twenty-five different potato genotypes generally used as parents were taken from the breeding programme of the Central Potato Research Institute, Shimla for a combining ability study. These genotypes included Indian advance generation breeding lines (JN 1752, E 4451, E 4486, JEM/O 30, JF 4841, JN 2207, JV 67, JX 90, MS/92-1090, MS/92-3128 and JN 1197), a released Indian cultivar (Kufri Bahar) and exotic *Solanum tuberosum* genotypes (CP 1338, CP 1358, CP 1909, CP 2093, CP 2161, CP 2283, CP 3290, CP 3356, CP 2013 and CP 3125) and Andigena genotypes (JEX/A 592, JEX/A 827 and JEX/A 1192). CP 1338 (unknown), CP 1358 (Idaho, United States of America), CP 1909 (B6532-10, United States of America), CP 2093 (71130.5, France), CP 2161 (Pentland Hawk, United Kingdom), CP 2283 (Geographe, Australia), CP 3290 (Hopehely, Hungary), CP 3356 (88076, Peru), CP 2013 (Atzimba, Mexico) and CP 3125(SR.1, Peru) were the exotic genotypes with donor's culture name/number and donor country mentioned in parentheses. Presence of major resistance (R) gene were reported in Atzimba (Pathogen tested list of potato cultivars for distribution. CIP Lima, Peru) and Pentland Hawk (European cultivated potato database: Cultivars and breeding lines, 2001. ECP/GR Potato Working Group). Most of the Indian breeding lines and cultivar Kufri Bahar were bred for characteristics like tuber yield and other acceptable tuber characters. None of these Indian breeding lines and cultivar Kufri Bahar was specifically bred for race-specific resistance to late blight.

Experimental plan

Plants were grown and crossed during the summer of 2002 at the Central Potato Research Station, Kufri (31°08′N, 77°18′E, 2,530 masl). Nineteen female (CP 1338, CP 1358, JN 1752, CP 1909, CP 2093, CP 2161, CP 2283, CP 3290, CP 3356, E 4451, E 4486, JEM/O 30, JF 4841, JN 2207, JV 67, JX 90, Kufri Bahar, MS/92-1090 and MS/92-3128) and six male (CP 2013, CP 3125, JN 1197, JEX/A 592, JEX/A 827 and JEX/A 1192) parents were used in line × tester mating design. Raising of seedlings and subsequent evaluation in clonal generations was done at the Central Potato Research Station, Jalandhar (31°02′N, 75°02′E, 237 masl). True potato seeds (TPS) of the 114 progenies were treated with 2,000 ppm gibberellic acid (GA_3) for 24 h for dormancy breaking. After drying in shade TPS were sown in seedling trays filled with 1:1 mixture of sand and farmyard manure during last week of September 2002. Seedlings at the three- to four-leaf stage were transferred individually to small polythene bags

for further growth. Finally, 60 seedlings of each cross at the six- to seven-leaf stage were transplanted to the field. The seedlings of a single progeny were planted together. At harvest, three tubers per seedling for each of the 45 randomly selected genotypes per progeny were retained to form three replications of the first clonal generation in next autumn (October–December) crop season. The same procedure was applied to form material for a second (SCG) and third clonal generation material (TCG) in successive autumn crop seasons. The planting material used for raising spring (January–April) crops was the produce of autumn crop season where the healthy crop could be raised in disease free conditions. Evaluation of progenies and parents in SCG and TCG were done in Randomized Block Design in 2005 and 2006 spring crop seasons, respectively. Experiments were laid out in three-row plots with three replications. Each row contained 15 plants. There were 45 genotypes planted together per progeny in each replication. The intra and inter row distances were 20 cm and 60 cm, respectively. Highly late blight susceptible cultivars Kufri Chandramukhi and Kufri Ashoka were planted after every 15 rows to act as a checks and spreader. Normal cultural practices were followed. However, no control measure was taken against late blight. No artificial inoculation was required as the late blight appears in severe form in spring crops every year in north Indian plains. Data were recorded on late blight severity as percentage of foliage covered with late blight, beginning on 16 February and subsequently at 4-day intervals. Observations were taken until there was 100% late blight infection in susceptible checks viz., Kufri Chandramukhi and Kufri Ashoka in order to serve as an anchor point for comparison. In total four observations were taken in a period of 12 days. The area under the disease progress curve (AUDPC) was calculated for each plot using the method of Shaner and Finney (1977).

Statistical analyses

Regression and step-wise regression of AUDPC on percentage foliage covered with late blight at different dates of observation were computed based on data from 114 progenies and 25 parents. Before analysis of variance, the normality of the data was tested by determining the relationship between mean and variance/standard deviation. Absence of any such relationship indicated that there is no need of data transformation. Homogeneity of error variance was tested by F max-test. Analysis of variance for parents and progenies was done on the data pooled over two years. Combining ability analysis was carried out based on Kempthorne (1957). Data pooled over two years on 17 females, four males and their 68 progenies from line × tester mating design were used for combining ability analysis and parent-progeny correlations. Two males viz., CP 2013 and JEX/A 592; two females viz., CP 2161 and MS/92-3128; and their progenies were not used for combining ability for quantitative resistance to late blight as these reflected qualitative resistance to late blight. A random effect model was used to test the significance of the combining ability variances, general combining ability (GCA) effects and specific combining ability (SCA) effects.

Heterosis was calculated with the following formula:

$$\text{Heterosis}\ (\%)\ = 100(F_1 - \text{MP})/\text{MP}$$

F_1 is the mean value of the hybrid progeny. MP is the average value of two parental clones.

Simple correlation coefficients (r) were calculated between parents and progenies. Averages of all 68 progenies were correlated to all mid-parent values to calculate mid-parent progeny correlation. GCA of all 21 parents was correlated to all parent per se values.

Results

The AUDPC values varied from 104 to 887 for the progenies and from 162 to 900 for the parents (per se). The progress of disease with time for some of the parents during Spring 2005 and Spring 2006 is shown in Fig. 1. The regression of AUDPC calculated from all the four observations on percentage blighted foliage area as observed at four different dates showed that date 3 (8 days

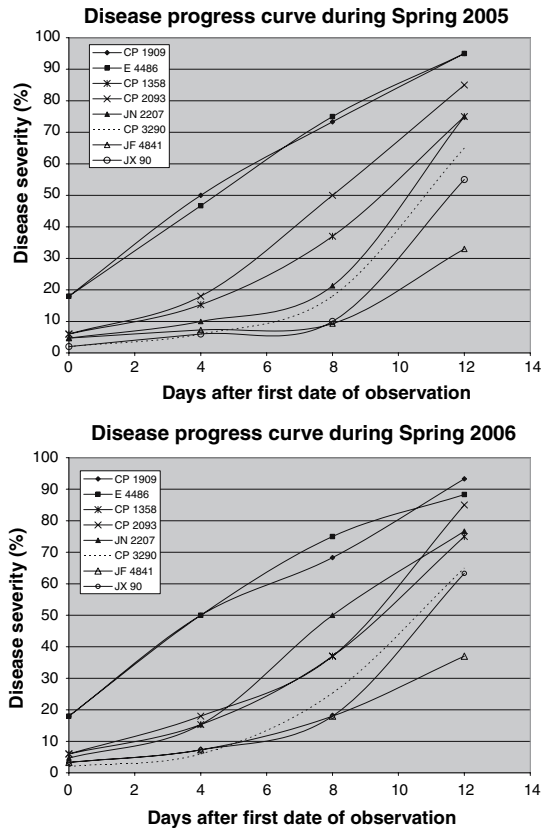

Fig. 1 Progress of late blight in some parents during Spring 2005 and 2006 crop seasons

after first observation) late blight observation has maximum relative contribution to the AUDPC as it accounted for 93–95% of the total variation in AUDPC (Table 1). The second most important date for late blight observation was date 2 (4 days after first observation) observation which explained 85–86% of total variation in AUDPC. The other two dates of observations (date 1 and date 4) were relatively less important. Stepwise regression analysis showed that the observations at date 3 and date 2 jointly accounted for 99% variation in AUDPC. The inclusion of date 4 and/or date 1 observation contributed little to R^2 value.

The progenies of parents CP 2013, JEX/A 592, CP 2161 and MS/92-3128 showed segregation in distinct resistance classes, while no such segregation was observed in progenies of all other parents.

Analysis of variance

Analysis of variance for 68 progenies and 21 parents showed that mean square due to years, parents and progenies were significant (Table 2). Interactions of parents and progenies with year were also significant. Parent versus progeny and its interaction with year were also significant.

Combining ability analysis showed that differences between progenies due to female and male parents were significant (Table 3). The female × male interaction was also significant. The estimates due to female × year and female × male × year interactions were also significant.

Table 1 Relationship of area under disease progress curve (AUDPC) with percentage diseased foliage at different dates of observations

Contribution of individual dates of observations (predictor) to AUDPC						
Date	Percent contribution of predictor to R^2 value based on all four dates			R^2 based on simple regression coefficients		
	2005	2006	Pooled	2005	2006	Pooled
Date 1	6.67	7.47	7.03	0.72	0.70	0.71
Date 2	32.44	33.54	32.92	0.86	0.85	0.86
Date 3	46.58	44.37	45.61	0.95	0.93	0.94
Date 4	14.31	14.61	14.44	0.71	0.73	0.72

R^2 based on stepwise regression coefficients			
	R^2		
	2005	2006	Pooled
Date 3	0.95	0.93	0.94
Date 3 & 2	0.99	0.99	0.99
Date 3, 2 & 4	1.00	1.00	1.00
Date 3, 2, 4 & 1	1.00	1.00	1.00

Table 2 Analysis of variance for parents and progenies

Source	Degrees of freedom	Mean square
Years	1	3066.49*
Replications in years	4	79.58
Parents	20	333700.00**
Progenies	67	170818.90**
Parents vs. progenies	1	110432.00**
Parents × year	20	2210.29**
Progenies × year	67	4555.55**
Parents vs. progenies × year	1	2293.51*
Error	352	489.03
Total	533	

Significant at *$p < 0.05$ and **$p < 0.01$

Estimates of variance components

The estimate of variance due to GCA (σ^2_{gca}) was of higher magnitude than variance due to SCA (σ^2_{sca}) (Table 4). The proportions of variances due to GCA to total genetic variance were 0.59, 0.63 and 0.63 for the years 2005, 2006 and pooled data of both the years, respectively.

General and specific combining ability effects

JX 90, JF 4841, CP 3356, CP 1358 and CP 3290 among females and JN 1197 and CP 3125 among males possessed good GCA for quantitative resistance to late blight (Table 5). JEM/O 30, CP 1338, CP 1909, E 4451, JV 67, MS/92-1090, E 4486, JEX/A 827 and JEX/A 1192 possessed poor GCA for resistance to late blight. Two crosses JV 67 × JEX/A 1192 and CP 1909 × JEX/A 827 had significant and high SCA in desired direction. Cross CP 1358 × CP 3125 had significant and high SCA effects in undesirable direction. The top six crosses based on mean for late blight resistance were JX 90 × CP 3125 (AUDPC = 211.3), JX 90 × JN 1197 (AUDPC = 273.3), CP 1358 × JN 1197 (AUDPC = 252.0), CP 3290 × JN 1197 (AUDPC = 266.0), CP 3356 × CP 3125 (AUDPC = 287.0) and JF 4841 × JN 1197 (AUDPC = 308.7) (Table 6). All these crosses had significant mid-parent heterosis in desired direction ranging from –15.24 to –49.2%.

Parent progeny correlations

GCA-parent per se, mid-parent-progeny, SCA-mid-parent heterosis and SCA-progeny correlations were highly significant (Table 7). GCA-parent per se, mid-parent-progeny and SCA-mid-parent heterosis correlations were high. SCA-progeny correlations were moderate.

Discussion

In India late blight appears in epiphytotic form almost every year. In the north Indian plains, in the main autumn crop it occurs in mild to moderate form but occasionally, assumes epiphytotic proportions (Singh and Shekhawat 1999). However in the spring crop (January–April)

Table 3 Analysis of variance for combining ability

Source	Degrees of freedom	Mean square	Expected mean squares
Years	1	634.67	
Replications in years	4	77.80	
Females	16	320789.70**	$\sigma^2_e + 3\sigma^2_{F\times M\times Y} + 4\times 3\ \sigma^2_{F\times Y} + 3\times 2\ \sigma^2_{F\times M} + 4\times 3\times 2\ \sigma^2_F$
Males	3	1355442.00**	$\sigma^2_e + 3\sigma^2_{F\times M\times Y} + 17\times 3\ \sigma^2_{M\times Y} + 3\times 2\ \sigma^2_{F\times M} + 17\times 3\times 2\ \sigma^2_M$
Female × male	48	46789.98**	$\sigma^2_e + 3\sigma^2_{F\times M\times Y} + 3\times 2\ \sigma^2_{F\times M}$
Female × year	16	9623.01**	$\sigma^2_e + 3\sigma^2_{F\times M\times Y} + 4\times 3\ \sigma^2_{F\times Y}$
Male × year	3	3037.81	$\sigma^2_e + 3\sigma^2_{F\times M\times Y} + 17\times 3\ \sigma^2_{M\times Y}$
Female × male × year	48	2960.58**	$\sigma^2_e + 3\sigma^2_{F\times M\times Y}$
Error	268	532.09	σ^2_e

** Significant at $p < 0.01$

Table 4 Estimate of variance components

Source	Year		
	2005	2006	Pooled over years
σ^2_{gca} (females)	13299.08	10089.33	11139.05
σ^2_{gca} (males)	13693.34	11967.98	12829.17
σ^2_{gca} (pooled)	13618.24	11610.14	12507.24
σ^2_{sca}	9381.78	6846.03	7304.9
$\sigma^2_{gca}/(\sigma^2_{gca} + \sigma^2_{sca})$	0.59	0.63	0.63

in the northern plains the disease regularly appears in epiphytotic form due to conducive weather conditions. There are no chances of avoidance of disease due to its severity. Hence evaluation for late blight resistance was done under conditions most suitable for late blight appearance.

Segregation in distinct resistance classes in progenies of the parents CP 2013, JEX/592, CP 2161 and MS/92-3128 reflected the qualitative resistance to late blight in these parents. Presence of major resistance (R) gene may mask quantitative resistance to late blight. To avoid the possibility of masking of quantitative resistance, the parents having indications of carrying major genes viz., CP 2013, JEX/592, CP 2161 and MS/92-3128 were not included in estimating variance components, combining abilities and parent-progeny correlations. Presence of other major R genes cannot be completely ruled out. But these major R genes, if present, might have been overcome by complex races of the fungus present in this region (Singh and Shekhawat 1999). The AUDPC values in 68 progenies from crosses of 17 female parents with four male parents in line × tester mating design, in the present study showed continuous variation, indicating thereby that the resistance in present study may be due to involvement of many minor genes. Similar results have been reported earlier (Canizares and Forbes 1995; Gopal and Singh 2003/4). In Potato the race-specific approach has turned out not to be durable, because of appearance of compatible races of *Phytophthora infestans* (Turkensteen, 1989; Umaerus and Umaerus 1994). Race-non-specific resistance to late blight in potato appears to be more stable and durable, but it provides only partial protection (Thurston, 1971; Haynes et al. 1998; Landeo et al. 2000b). This type of resistance

Table 5 Estimates of general combining ability (GCA) and specific combining ability (SCA) effects for quantitative resistance to late blight measured as area under disease progress curve

Parents		SCA effects				GCA effects (females)
Female	Male	CP 3125	JN 1197	JEX/A 827	JEX/A 1192	
CP 1338		–124.10	120.19	5.05	–1.14	118.77**
CP 1358		135.48*	–100.23	36.30	–71.56	–100.81**
JN 1752		–26.02	–78.73	15.47	89.27	–32.31
CP 1909		106.15	–70.23	–146.03*	110.11	115.85**
CP 2093		–32.77	–84.14	14.05	102.86	42.10
CP 2283		–98.10	–6.48	39.72	64.86	–1.23
CP 3290		33.98	–96.73	114.80	–52.06	–90.31*
CP 3356		–97.10	1.19	19.05	76.86	–119.56**
E 4451		63.23	89.52	–38.61	–114.14	105.44**
E 4486		73.48	67.11	–77.70	–62.89	77.85*
JEM/O 30		99.40	–56.98	55.89	–98.31	129.27**
JF 4841		–16.10	26.19	–11.95	1.86	–170.56**
JN 2207		3.31	–30.06	5.80	20.94	–52.65
JV 67		–19.69	98.27	102.14	–180.73**	91.35*
JX 90		–35.19	41.77	14.64	–21.23	–257.48**
Kufri Bahar		14.40	37.36	–62.45	10.69	65.27
MS/92-1090		–80.35	41.94	–86.20	124.61	79.02*
GCA (males)		–71.65**	–122.61**	117.53**	76.73**	

Significant at *$p < 0.05$ and **$p < 0.01$

– and +: Combining ability effects for resistance in desired and undesired directions

Table 6 Mean area under disease progress curve (AUDPC) values of parents and progenies for quantitative resistance to late blight

Parents		AUDPC value for progenies				AUDPC value for female parents
Female	Male	CP 3125	JN 1197	JEX/A 827	JEX/A 1192	
CP 1338		498.7	692.0	817.0	770.0	856.0
CP 1358		538.7	252.0	628.7	480.0	371.3
JN 1752		445.7	342.0	676.3	709.3	334.7
CP 1909		726.0	498.7	663.0	878.3	707.7
CP 2093		513.3	411.0	749.3	797.3	428.0
CP 2283		404.7	445.3	731.7	716.0	316.0
CP 3290		447.7	266.0	717.7	510.0	244.7
CP 3356		287.3	334.7	592.7	609.7	357.3
E 4451		672.7	648.0	760.0	643.7	739.3
E 4486		655.3	598.0	693.3	667.3	712.7
JEM/O 30		732.7	525.3	878.3	683.3	862.7
JF 4841		317.3	308.7	510.7	483.7	162.0
JN 2207		454.7	370.3	646.3	620.7	354.3
JV 67		575.7	642.7	886.7	563.0	726.0
JX 90		211.3	237.3	450.3	373.7	206.3
Kufri Bahar		583.7	555.7	696.0	728.3	786.0
MS/92-1090		502.7	574.0	686.0	886.0	427.3
AUDPC value for male parents		625.7	566.3	898.3	694.7	

Table 7 Some important parent progeny correlations

Combination	Correlation coefficient		
	2005	2006	Pooled
GCA-parent per se	0.797**	0.803**	0.809**
Mid-parent-progeny	0.748**	0.752**	0.760**
SCA-progeny	0.458**	0.441**	0.443**
SCA-mid-parent heterosis	0.690**	0.668**	0.681**

** Significant at $p < 0.01$

is characterized by continuous variation in phenotypic appearance and complex polygenic inheritance (Black, 1970; Umaerus 1970). Race-non specific resistance also called horizontal resistance is difficult to separate indisputably from race-specific-resistance called vertical resistance (Johnson 1979; Turkensteen 1989).

The evaluation of progenies and parents for late blight resistance may have year-to-year variation and it is better to evaluate these at least for 2 years (Gopal and Singh 2003/2004). Keeping this in view evaluation for late blight resistance under field condition was done over 2 years, using plants of two (SCG and TCG) clonal generations. In the present study also the effect of year was found to be significant. Non-significant replication effect suggested that infection under field condition was uniform and satisfactory. Non-significant replication effect for late blight has also been reported earlier (Simmonds and Wastie 1987; Kaushik et al. 2000; Gopal and Singh 2003/2004). The parent versus progeny mean sum of squares was statistically significant meaning thereby that average mid-parent heterosis was significant.

A random effect model was used for studying the combining ability variances and effects so that they have broad application for future breeding programmes. Both additive and non-additive gene actions were important in inheritance of quantitative resistance to late blight. However, GCA variances were of higher magnitude than SCA variances. Predominantly additive gene action for quantitative resistance to late blight was also reported by earlier workers (Tai and Hodgson 1975; Malcolmson and Killick 1980; Stewart et al. 1992; Wastie et al. 1993). Higher SCA variances than GCA variances for late blight resistance were also reported by some workers (Killick and Malcolmson 1973; Kaushik et al. 2000). Landeo et al. (2000a) reported almost equal importance of both non-additive and additive gene action for horizontal resistance in a potato breeding population B3C1. The difference in proportion of GCA and SCA variances in

various studies could be attributed to differences in genetic material used. In the present study, a total of 21 genotypes representing different types were used to get the proper and reliable estimate of variance components for quantitative resistance to late blight.

The GCA has a conceptual implication that each line being evaluated is tested against a random sample of some specific population. In the present study parents had large differences for GCA (Table 5). Large differences between parents for their GCA for quantitative resistance to late blight were also reported by earlier workers (Tai and Hodgson 1975; Malcolmson and Killick 1980; Stewart et al. 1992; Wastie et al. 1993; Kaushik et al. 2000). The top six promising crosses for late blight resistance had both parents with good GCA. This shows the importance of selecting parents based on GCA. The parents and crosses found promising based on combining ability in the present study may be useful for developing late blight resistant genotypes in other breeding programmes also as all the conclusions about their combining abilities were based on random effect model.

High GCA-parent per se and mid-parent progeny correlations show that per se performance does give an idea about the GCA of a parent. However, parental performance cannot be used completely in predicting mean performance of the progeny. High GCA-parent per se correlation was also reported by Steward et al. (1992).

Only those dates of observations which fell within the period of rapid increase in disease were found important in recording late blight reaction, as the dates 3 and 2 observations contributed the most towards the variation in AUDPC value based on all four observations. Therefore this period of late blight growth can be used for recording observations on late blight severity if it is not possible to take multiple observations especially when large numbers of genotypes are to be studied. The second date of observation as most important date was reported by Gopal and Singh (2003/2004). Haynes and Weingartner (2004) reported that the AUDPC from two data points may provide as much information as from repeated assessments as long as one date was shortly after the epidemic started and the other date was as the epidemic was reaching its peak. However, in our study two dates (date 3 and date 2) during the rapid progressive stage of disease were as informative as all the 4 assessments and the initial and last observations were found to be of little use. The differences may be due to the total period of the epidemic and/or the stage at which the observation recording started.

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