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RELIABILITY OF DIFFERENT PARAMETERS TO ESTIMATE RELATIVE FOLIAGE BLIGHT RESISTANCE AND ITS RELATION TO MATURITY IN POTATO

ABSTRACT

A comparative study of different parameters calculated for foliage resistance of potato to *Phytophthora infestans* (Mont.) de Bary was conducted on the data for 27 cultivars and one prebreeding clone in field assessment in 2003 at BAZ Groß Lüsewitz. Relationships between the parameters and maturity were determined by linear regression. The strongest associations with maturity were found for the relative area under the disease progress curve (RAUDPC), delay of attack, and attack on a determined date (r^2 = 0.47–0.52). The least association with maturity was found for foliage blight resistance at Groß Lüsewitz, FBR_{GL} (r^2 = 0.03), calculated by using a maturity–dependent section of the disease progress curve. The apparent infection rate (AIR), RAUDPC and delay of attack could only explain below 50% of variability of $FBR_{GL.}$ The method for calculation of foliage resistance in breeding developed at BAZ and named FBR_{GL} is described in detail, and the usefulness of the different methods for evaluation of resistance, management of plant protection and breeding is discussed.

Key words: breeding, foliage blight, methods, potato, *Phytophthora infestans*, resistance

INTRODUCTION

Relative or quantitative resistance of potato to *Phytophthora infestans* (Mont.) de Bary is assumed to be polygenically determined and long lasting (Wastie 1991, Darsow 2000, Schöber–Butin 2001). It is a multifaceted trait that operates through different mechanisms and seems to be influenced by factors regulating basic processes of the plant such as physiological age. There is comprehensive literature evidencing the association of lateness with foliage resistance (Van der Plank 1957, Toxopeus 1958, Colon 1994). This association may be explained either by genetic linkage between genes for maturity and resistance or by influence on expression of resistance genes.

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Visker *et al.* (2002) detected maturity–linked QTL (quantitative trait loci) for foliage blight resistance as well as those not linked with maturity. Mechanisms and inheritance of various components of resistance are largely unexplained. Relative foliage blight resistance is assumed to be difficult, if not impossible, to combine with earliness in new potato cultivars (Wastie 1991, Colon 1994). In this respect there is consensus in literature and among most practical breeders. Muskens and Allefs (2002) formulated: "Although progress has been made, the apparently unbreakable linkage between partial resistance and late maturity implies a severe barrier for successful application of this type of resistance." The reasons for such a view are common insufficiencies both in methods used for estimation of resistance and in applied breeding methods (Darsow 2002a). However, contrary to the opinion cited above, the progress in combining foliage blight resistance and earliness by conventional breeding at BAZ Groß Lüsewitz is very promising, and the correlation with lateness is no longer a barrier (Darsow 1999, 2000, 2002a, 2002b).

This paper is focused on methodical details of assessment of resistance. A reliably characterised foliage blight resistance is a precondition both for breeding and minimising the application of fungicides in management of plant protection. Whilst separation of true resistance from maturity effects on attack is essential for breeding, cultivar–specific reactions as a delay of attack or increase of attack in time are of interest for decision of fungicide application.

MATERIAL AND METHODS

Evaluation of foliage blight resistance by different methods

In quantitative estimation of foliage blight resistance it is commonly used to calculate an area under disease progress curve (Fry 1978, Colon 1994, Dowley *et al.* 1999). In this study primary disease data were uploaded to Web–blight for calculation of a delay of attack, apparent infection rate (AIR), and the relative area under the disease progress curve (RAUDPC) (http://www.web–blight.net; Hansen *et al.* 2002, 2003). Additionally, resistance was calculated using a maturity–dependent section of the disease progress curve. This method is named FBR_{GL} and it was developed at BAZ (Darsow 1989).

Apparent infection rate, AIR

This parameter represents the slope of the disease progress curve, assuming that this curve can be approximated by a logistic function. This slope is estimated by calculating the regression of:

$$\frac{\ln x}{(1-x)}$$

where

x is the proportion of affected tissue (Fry 1977).

Regressions are calculated for the intervals in which the disease (x) progresses from 1% to 99% (Hansen *et al.* 2002).

Relative area under the disease progress curve, RAUDPC

Together with the final disease rating and the apparent infection rate, this estimate gives a comprehensive description of crop resistance (Hansen *et al.* 2002). First, the area under the disease progress curve (AUDPC) is calculated as proposed by Shaner and Finney (1977):

$$AUDPC = \Sigma\left(\frac{x_{i+1} + x_i}{2}\right) \times \left(t_{i+1} - t_i\right)$$

where

x_i is the proportion of tissue affected at the i–th observation,

and

t is the time in days after inoculation at the i–th observation.

The index i runs from 1 to n, where n is the total number of observations. Values for AUDPC are normalised by dividing the AUDPC by the total area of the graph, i.e. the number of days from inoculation to the end of the observation period × 1.0. This normalisation results in the relative AUDPC (Fry 1978, Flores–Gutiérrez and Cadena–Hinojosa 1996).

Delay of attack

A delay in the disease onset (days) for each variety or clone was compared to the date of first attack in the trial.

Calculation of resistance by using a maturity–dependent section of disease progress curve, named foliage blight resistance at Groß Lüsewitz (FBR_{GL})

Herein it is necessary to describe the method as a whole, because earlier information (Darsow 1989, 1999, 2003) is not well known. The field to assess foliage blight resistance has to be isolated from other potato production. Surrounding by hemp prolongs the duration of wetness of foliage and reduces neighbour effects by wind within the trial and to outside. The clones are grown in plots with 2 rows, 6 plants each. If the clones are grouped according to their maturity, and susceptible and more resistant clones are not mixed within the groups, the falsifying neighbour effects are, for the most part, avoided. Plots with two or three rows give a lower statistical error. Without replication we obtained an LSD of 1.3 scores in a 1–9 scale for comparison of clones in an average of 3 year–test (Darsow 1989).

Inoculation was carried out after 8 p.m. on July 10, including 454 plots. A mixture of three isolates with virulence gene combination 1.2.3.4.5.6.7.8.9.10.11, 1.2.3.4.5.6.7.(8.)9.10.11 and 1.2.3.4.5.7.(8.)10.11 from BBA Braunschweig was used. Only 1–2 leaves per clone near the ground in the furrow were inoculated by spraying the lower surfaces of leaves. Disease assessments were started five days after inoculation and performed twice a week. The pathogen infectibility was supported by irrigation.

Potato cultivars Adretta, Karlena, Kuras, Mariella, Maxilla, Bintje and others, recommended by Dowley *et al.* (1999), were used as long–term standards. Moreover, some own quite resistant early to second early clones, like BAZ–GL–77.6669.158, helped to select a suitable section of the disease progress curve according to maturity, to calculate the resistance.

The principle of our calculation of blight resistance was, as the first step, separation of the resistance from effects of maturity. Therefore, maturity data for two years or more are taken from the breeding garden. An exact estimation of maturity in a scale 1–9 is important for the calculation. Only a section of the disease progress curve is selected in dependence on maturity. The average of daily scores of attack (% of attacked foliage was transferred to score 1–9) in this section is the score of resistance. During a season, 14–17 observations enable to calculate daily data of attack. For instance, the section July 31 – August 6 was selected for cv. Adretta, which gave the expected level of resistance as years before. Cv. Adretta has maturity of 6.6, and for such maturity the section of the curve from July 31 – August 5 was fixed to calculate resistance of all clones of exactly the same maturity (see Table 1, first variant). For cv. Bintje, the section of August 7–15 was selected, resulting in the resistance near score 1, and was fixed for maturity of 4.0. Between both scores of maturity the running of sections from July 31 to August 7 has to be divided, as it is shown in Table 1, variant 1. The later the maturity is, the later starts the section, and the longer is the used part of the curve. But September 17 was the last date of observation and defoliation. The calendar has to be continued up to very early and extremely late. A coefficient of correlation $r = -0.26$ in variant 1 was considered to be too high. Therefore, additional variants were calculated with changed sections of the disease progress curve. One of these was variant 2 in Table 1. The changed calendar is tested and adjusted to additional standard cultivars, which should receive more or less their expected levels of resistance. Their maturity scores give fixed sections between those for cvs Adretta and Bintje. Then, for the whole material the calculation was repeated and the correlation between resistance and maturity estimated. The sections for cvs Adretta and Bintje were changed not too much, but the dynamics was changed on the whole. Less suitable conditions for spread of late blight in the middle of August are considered in the second variant by selecting a delayed section of disease progress curve (DPC) in second late and late clones. High infection pressure in a rainy period is to be considered by reducing the section of the DPC. Low pressure enables greater steps in days between the maturity values and/or prolonging the section. So this method can flexibly include the disease dynamics.

Table 1

Calendar for calculation of foliage blight resistance FBR_{GL} in 2003

Maturity	Section of DPC variant 1		Section of DPC variant 2	
	Period	Number of days	Period	Number of days
9.0	25.07. – 28.07.	4	25.07. – 28.07.	4
8.8	25.07. – 29.07.	5	25.07. – 29.07.	5
8.6	26.07. – 30.07.	5	26.07. – 29.07.	4
8.4	26.07. – 31.07.	6	26.07. – 30.07.	5
8.2	27.07. – 31.07.	5	26.07. – 31.07.	6
8.0	28.07. – 01.08.	5	27.07. – 31.07.	5
7.8	29.07. – 01.08.	4	28.07. – 31.07.	4
7.6	29.07. – 02.08.	5	28.07. – 01.08.	5
7.4	29.07. – 03.08.	6	29.07. – 01.08.	4
7.2	30.07. – 03.08.	5	29.07. – 02.08.	5
7.0	30.07. – 04.08.	6	29.07. – 03.08.	6
6.8	30.07. – 05.08.	7	30.07. – 03.08.	5
6.6	31.07. – 05.08.	6	30.07. – 04.08.	6
6.4	31.07. – 06.08.	7	30.07. – 05.08.	7
6.2	01.08. – 06.08.	6	31.07. – 05.08.	6
6.0	01.08. – 07.08	7	31.07. – 06.08.	7
5.8	01.08. – 08.08	8	01.08. – 06.08.	6
5.6	02.08. – 08.08	7	01.08. – 07.08	7
5.4	02.08. – 09.08.	8	01.08. – 08.08	8
5.2	03.08. – 09.08.	7	02.08. – 08.08	7
5.0	03.08. – 10.08.	8	02.08. – 09.08.	8
4.8	04.08. – 10.08.	7	03.08. – 09.08.	7
4.6	04.08. – 12.08.	9	04.08. – 10.08.	7
4.4	05.08. – 13.08.	9	05.08. – 14.08.	10
4.2	06.08. – 14.08.	9	07.08. – 16.08.	10

Table 1

Continued

Maturity	Section of DPC variant 1		Section of DPC variant 2	
	Period	Number of days	Period	Number of days
4.0	07.08.–15.08.	9	09.08.–18.08.	10
3.8	08.08.–16.08.	9	11.08.–22.08.	12
3.6	09.08.–17.08.	9	15.08.–23.08.	9
3.4	10.08.–18.08.	9	19.08.–29.08.	11
3.2	12.08.–20.08.	9	23.08.–03.09.	12
3.0	15.08.–25.08.	11	27.08.–07.09.	12
2.8	19.08.–29.08.	11	01.09.–11.09.	11
2.6	25.08.–05.09.	12	07.09.–16.09.	10
2.4	01.09.–14.09.	14	11.09.–17.09.	9
2.2	10.09.–17.09.	8	15.09.–17.09.	3
2.0	12.09.–17.09.	6	17.09.	1
1.8	14.09.–17.09.	4	17.09.	1
1.6	16.09.–17.09.	2	17.09.	1
1.4	17.09.	1	17.09.	1
1.2	17.09.	1	17.09.	1
1.0	17.09.	1	17.09.	1
Mat./Res.	r = −0.25606		r = −0.118	

Material

This paper considers 27 tested cultivars and one prebreeding clone of BAZ. Cultivar Eersteling was the earliest one, whilst cvs Adretta, Erntestolz, Gala, Gloria, Karlena, Marabel and Pirol had been estimated to be early. Cultivars Beluga, Melina, Resy and Tomensa are early to second early; Maxilla, Presto, Satina, Sempra, Steffi and White Lady are second early; Apart, Granola, Bintje and Naturella are second early to second late; Cara, Irene and Jelly belong to the second late group; Enterprise and Kuras were found to be late. The following differentials: *r, R1*, *R2*, *R3*, *R4*, *R6*, *R7*, *R8*, *R11* were included to observe the acting virulence. Only virulence gene 8 occurred very late. *R5*, *R9* and *R10* were not grown because of a heavy virus attack.

RESULTS AND DISCUSSION

The results of field assessment of blight resistance in 2003 enabled an analysis of correlation beetween particular resistance parameters as well as between the parameters and maturity (Table 2).

Table 2

Correlation between parameters of resistance and maturity in the assessment done in 2003, calculated with 27 varieties and one prebreeding clone

Trait 1	Trait 2	Correlation coefficient r	$r^2 \times 100$ [%]
Maturity	FBR_{GL}	−0.18044810	3.3
Maturity	RAUDPC	0.72198060	52.1
Maturity	AIR	0.53410955	28.5
Maturity	Delay of attack	−0.68751873	47.3
Maturity	Attack 08.08.03	0.69948184	48.9
FBR_{GL}	RAUDPC	−0.68084469	46.4
FBR_{GL}	AIR	−0.64983314	42.2
FBR_{GL}	Delay of attack	0.61259319	37.5
FBR_{GL}	Attack 08.08.03	−0.72303192	52.3
RAUDPC	AIR	0.59432455	35.3
RAUDPC	Delay of attack	−0.86462902	74.8
RAUDPC	Attack 08.08.03	0.97986814	96.0
AIR	Delay of attack	−0.58310141	34.0
AIR	Attack 08.08.03	0.62862649	39.5
Delay of attack	Attack 08.08.03	−0.87061444	75.8

All correlation coefficients proved to be significant, except that between maturity and FBR_{GL}. The least association with maturity was found for FBR_{GL}, where only 3% influence was detected. About 28% of the variation in AIR could be explained by maturity. A stronger association with maturity was found for the attack on 8^{th} August (48,9% of variation could be explained by maturity), delay of attack and RAUDPC (47,3% and 52,1% explained by maturity, respectively). A high correlation between resistance parameters was found for RAUDPC with delay of attack (r^2 = 74,8%), RAUDPC with attack on August 8^{th} (r^2 = 96%), and delay of attack with attack on August 8^{th} (r^2 = 75,8%).

The next step of analysis was done by grouping the clones according to their maturity, in which the groups had a span of variation of one score (Fig. 1, Table 3). The single clone in the third line of Table 3 is an example of successful breeding with durable resistance since 20 years; it is the first clone in Table 1. Fig. 1 gives the average of maturity of each group on the right side. The later the maturity is, the lower is the slope of the curve. Only the prebreeding clone is the exception, having a curve similar to that for the second late group. The arrows on each curve mark the beginning and the end of the section used for calculation of FBR_{GL}.

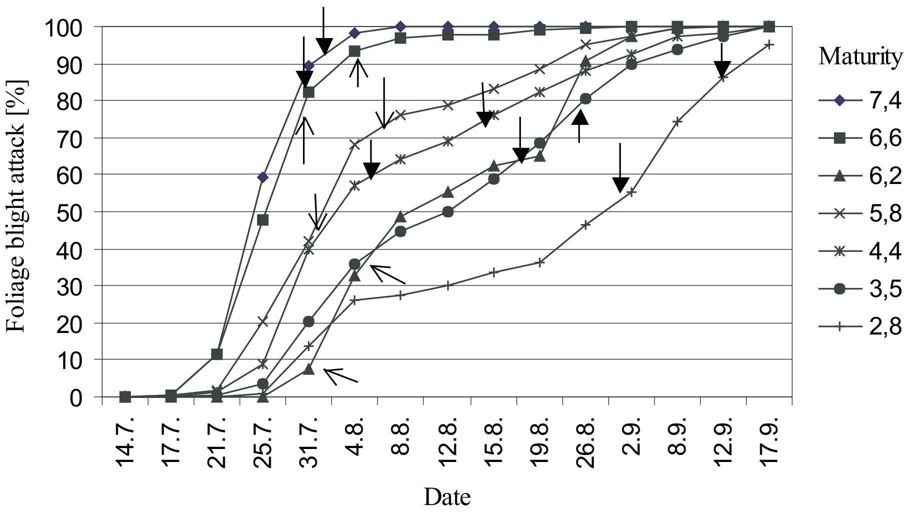

Fig. 1. Foliage blight progress curves (mean values) for clones grouped according to their maturity, grouped in steps of one score. Maturity score 9: extremely early. Maturity score 6.2 belongs to a single (nearly) early, stable resistant clone. The arrows indicate the section used for calculation of FBR_{GL}

Table 3

Parameters of resistance (mean value and standard deviation) in groups of clones according to maturity

Maturity	Number of clones	Attack [%] on 08.08.2003	FBR_{GL}	RAUDPC	AIR	Delay of attack
7.4	1	99.9	2.5	0.83	0.41	0.0
6.6	9	96.8 ± 6.0	2.8 ± 1.0	0.80 ± 0.04	0.40 ± 0.20	2.0
6.2	1	48.7	6.7	0.55	0.16	11.0
5.8	4	76.0 ± 20.7	4.5 ± 1.3	0.69 ± 0.08	0.21 ± 0.13	3.2
4.4	7	64.3 ± 23.1	4.3 ± 1.5	0.63 ± 0.10	0.16 ± 0.09	8.7
3.5	4	44.7 ± 22.4	3.9 ± 1.7	0.54 ± 0.10	0.13 ± 0.01	10.0
2.8	2	27.7 ± 38.2	3.7 ± 2.1	0.37 ± 0.30	0.17 ± 0.06	11.0

Maturity groups of 6.2 and 3.5 had similar curves, but for calculation of FBR_{GL} July 31 – August 5 and August 5–14 were used, respectively. The difference corresponds to the attacks of 23% and 71%. Additional information is provided in Table 3. The groups include 1–9 clones. In general, the later the varieties were, the lower was the attack on 8th of August, but the higher were the differences within the group. The same tendency can be found in RAUDPC. Selection according to RAUDPC for breeding purpose would have a chance in the late group, and it would remain the prebreeding clone. AIR showed a difference between the first two groups and the rest. The standard deviations of the second and fourth group (line) offer a chance for selection by a breeder according to AIR, whereas the other do not. In FBR_{GL} a steady increase of resistance with lateness cannot be observed, but a remarkable variability within the groups as sign for diversity of resistance and possibility for selection.

The presence of single clones showing similar maturity made possible to compare the parameters for blight resistance. Both, cvs Presto and Tomensa and clone BAZ–GL–77.6669.158 exhibited exactly the same maturity of 6.1–6.2 (Table 4). The highest differentiation for these three genotypes was given by FBR_{GL} (Fig. 2). In RAUDPC the difference between cvs Presto and Tomensa was not as clear as that in FBR_{GL}. Between cv. Tomensa and BAZ–GL–77.6669.158 marked differences in FBR_{GL}, RAUDPC and delay of attack occurred, but no difference was found in AIR (Table 4). On the other hand, although the difference in RAUDPC between cv. Tomensa and cv. Presto was smaller than that between cv. Tomensa and the BAZ clone, a very large difference in AIR between the clone and cv. Presto was found (0.14 and 0.85, respectively). With cv. Eersteling, the earliest among the genotypes tested (Table 4), and with cv. Presto similar curves, RAUDPC and delays of attack were

Table 4

Maturity and parameters of resistance of four clones

Potato cultivar/clone	Maturity	Attack [%] on 08.08.2003	FBR_{GL}	RAUDPC	AIR	Delay of attack
Eersteling	7.4	99.9	2.5	0.83	0.41	0
Presto	6.2	100.0	1.6	0.81	0.85	3
Tomensa	6.1	75.0	4.5	0.71	0.14	3
77.6669.158	6.2	48.7	6.7	0.55	0.16	11

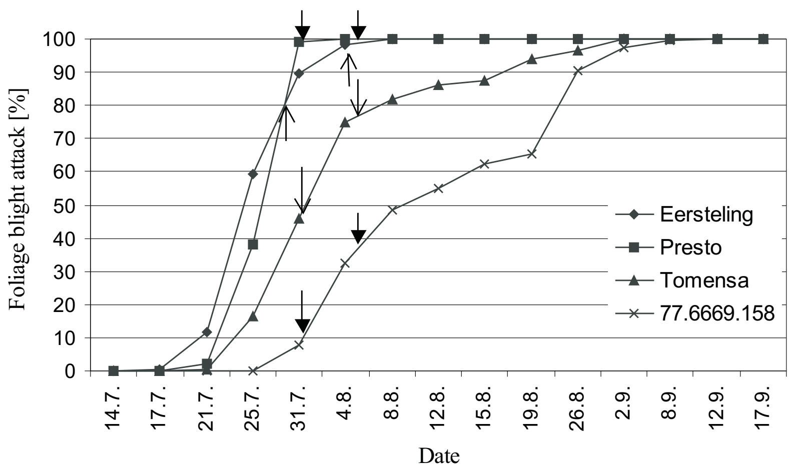

Fig. 2. Foliage blight progress curves of very early to early clones in field assessment in Groß Lüsewitz, 2003. The arrows indicate the section used for calculation of FBR_{GL}

obtained, but the difference in AIR was large (0.41 vs. 0.85). Cultivar Tomensa and the BAZ clone obtained the same AIR (0.14 and 0.16), but the values for RAUDPC and delay of attack greatly differed. The higher resistance to infection and lower sporulation caused the more gentle slope of the BAZ clone. These data are a good example evidencing that none of the resistance parameters alone should be used to make proper decisions on late blight protection. Considering these parameters together, including a graphic display of the disease progress curve, gives a much better characterisation of resistance than, for example, RAUDPC alone.

The next example to look at the details includes second early cvs Steffi, White Lady, Sempra and Satina, and second early to second late cvs Naturella and Bintje. All of them are included in the span of maturity scores of 4.8–4.0 (Table 5). This group contains a very wide range of variability of foliage blight resistance, from highly susceptible cv. Bintje, moderately resistant cv. Satina, up to low to moderately resistant cvs Steffi, White Lady, Sempra and Naturella. Certainly, the resistant cultivars show a more linear type of the disease progress curve, whilst the other express S–type curves (Fig. 3). The cvs Steffi, White Lady and Sempra with very similar maturity differ from each other by 0.6–1.8 scores in FBR_{GL}, 0.03–0.13 in RAUDPC, but not in AIR nor in a delay of attack (Table 5). Cultivar Bintje would be discarded, whichever of the parameters would be used for selection. Cultivar Satina would be eliminated by RAUDPC and FBR_{GL}, but it was surprisingly classified as quite resistant based on the AIR result. Selection according to AIR would only eliminate cv. Bintje. Using RAUDPC, cvs Bintje and Satina, and perhaps also White Lady and Steffi, would be discarded. It seems that the difference between FBR_{GL} and RAUDPC is smaller in more linear slope. $FBR_{GL,}$ compared to other variables, was found useful to determine a difference in the resistance between cvs Steffi and White Lady.

Table 5

Resistance parameters of six clones with similar maturity

Potato cultivar	Maturity	Attack [%] on 08.08.2003	FBR_{GL}	RAUDPC	AIR	Delay of attack
Steffi	4.8	48.0	5.2	0.57	0.11	11
White Lady	4.6	58.0	4.6	0.60	0.11	11
Sempra	4.7	28.3	6.4	0.47	0.13	11
Satina	4.5	86.3	3.0	0.73	0.19	7
Bintje	4.0	97.6	1.4	0.79	0.36	7
Naturella	4.0	12.0	6.4	0.39	0.14	11

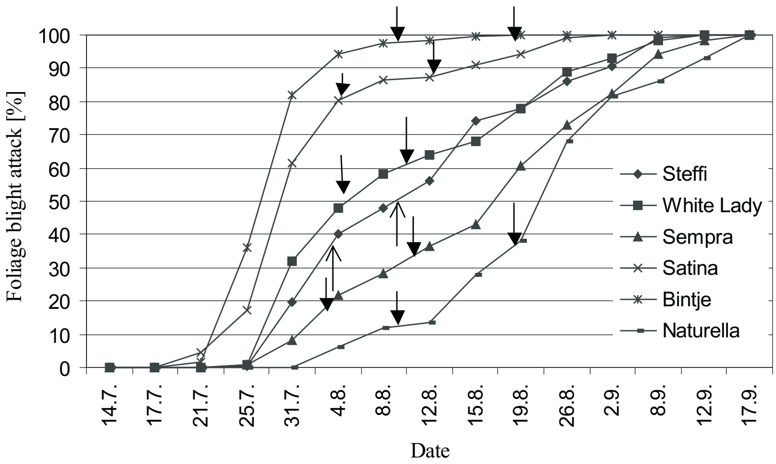

Fig. 3. Foliage blight progress curves of second early to second late clones, field assessment in Groß Lüsewitz, 2003. The arrows indicate the section used for calculation of FBR $_{GL}$

CONCLUSIONS

Having related different resistance parameters to maturity it was found that the RAUDPC values were highly correlated with this feature. This finding is not optimistic, as RAUDPC is widely used to estimate resistance of potato cultivars and clones to late blight for breeding purposes (Fry 1978, Colon 1994, Dowley *et al.* 1999, Kirk *et al.* 2001, Gans 2003). This makes the above cited view of Muskens and Allefs (2002) understandable. AIR was weaker associated with maturity than RAUDPC, which is difficult to explain. The reason is not that AIR is only calculated for disease assessments in the area from 1% to 99%. Only using a section of the curves selective according to maturity can overcome the correlation with maturity. In the method FBR_{GL} only a small section of the disease progress curve depending on maturity is used. This parameter was not associated with maturity at all, which is very important, especially in scoring for breeding purposes.

Our results suggest that an integrated use of several parameters obtained from disease data might be useful for plant protection management to reduce the methodical problems. A combination of RAUDPC, delay of attack and AIR is useful for identifying the delay of attack controlled by *R*–genes. For interpreting RAUDPC results it is possible to divide the material into maturity groups and evaluate the results for each group separately, followed by comparison of the results to well known test varieties. Moreover, the FBR_{GL} analyses a wide range of differences between the days of vegetation within the maturity groups by taking maturity as a continuous trait, estimated not only with 9 scores, but also with subunits between the full scores. Therefore, the FBR_{GL} method is best adapted for estimation of resistance. Yet, all resistance parameters in this study except the FBR_{GL} results were easily calculated by the Internet Web–Blight service, based on primary disease data. The disadvantage of the FBR_{GL} method is that it is empirical, and hence not very easy to apply elsewhere. Therefore, some steps will be taken to develop a new standardised FBR_{GL} method for evaluating foliar blight resistance under field conditions to be used together with other methods in computer programs and web–applications.

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