Testing potatoes for resistance to *Globodera pallida* pathotype Pa-3; resistance spectra of plant genotypes and virulence spectra of Pa-3 isolates

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SUMMARY

The multiplication of eleven isolates of *Globodera pallida* pathotype Pa-3 on twelve resistant clones and four standard varieties was compared. A significant main effect of plant-genotype, Pa-3 isolate and year on the number of cysts produced, was observed as well as a significant plant genotype/Pa-3 isolate interaction, plant genotype/year and Pa-3 isolate/year interaction. The resistant clones can be divided into two groups. In one group the resistance level based on the number of cysts produced decreases with an increase in average virulent level of the nematode isolate. In the second group, the resistance level does not vary with the virulent level of the Pa-3 isolates. In a separate experiment the effect of plant genotype and Pa-3 isolate (six standard varieties and four Pa-3 isolates) on the hatching characteristics of the cysts produced was studied. For both factors a significant effect was found. A significant difference in number of hatched juveniles was observed between the susceptible cultivars and the resistant standard cultivar AM 78-3778 as well as between the susceptible cultivars.

RÉSUMÉ

Tests concernant la résistance de la pomme de terre à Globodera pallida *pathotype Pa-3;*
spectres de résistance des génotypes de la plante et spectres de virulence d'isolats du pathotype Pa-3

La multiplication de onze isolats de *Globodera pallida* pathotype Pa-3 a été comparée sur douze clones et quatre variétés standard. Il a été observé un effet principal, significatif, du génotype de la plante, de l'isolat Pa-3 et de l'année de culture sur le nombre de kystes produits; de même ont été observées des interactions génotype de la plante/isolat Pa-3, génotype de la plante/année et isolat Pa-3/année. Les clones résistants peuvent être divisés en deux groupes. Dans l'un, le niveau de résistance, fondé sur le nombre de kystes produits, décroît en même temps que s'accroit le niveau moyen de virulence. Dans l'autre, le niveau de résistance ne varie pas en fonction du niveau de virulence des isolats Pa-3. Une expérience particulière a permis d'étudier l'effet du génotype de la plante et de l'isolat Pa-3 (six variétés standards et quatre isolats Pa-3) sur les caractères de l'éclosion hors des kystes produits. L'un et l'autre facteurs produisent un effet significatif. Il a été observé des différences significatives dans le nombre de juvéniles éclos entre les cultivars sensibles et le cultivar résistant standard AM 78-3778, ainsi qu'entre les cultivars sensibles eux-mêmes.

The first breakdown of resistance to pathotype Pa-2 of *Globodera pallida* was observed in 1975 in the starch potato growing area in the north-east part of the Netherlands. Large scale reproduction of *G. pallida* was observed on potato cyst nematode resistant varieties. After this observation various isolates of *G. pallida* which multiplied on " Pa-2 " resistant varieties have been collected. To identify their pathotype these isolates were tested on the Pa-2 differential (VTN)² 62-33-3. Isolates with reproduction rates larger than one were classified as " Pa-3 " pathotype populations. Isolates with reproduction rates less than one were classified as " Pa-2 " pathotype populations.

The tests showed that the Pa-3 isolates differed in reproduction rate on clone $(VTN)^2$ 62-33-3. Also in screening potato clones for Pa-3 resistance, differences in reproduction rate between the Pa-3 isolates were observed.

This paper presents the results of a resistance test of Pa-3-resistant potato clones and the standard differential potato clones with a representative sample of " Pa-3 " isolates. These results are employed for the selection of a *Solanum* genotype with Pa-3 resistance to be incorporated in a differential test set for the identification of new virulence groups of *G. pallida* and to be used as a standard in screening for Pa-3 resistant potato clones.

Material and methods

Twelve potato clones (AM clones) with resistance to *Globodera rostochiensis*, pathotypes Ro-1, 4, Ro-2, 3 and Ro-5 and with resistance to *G. pallida*, pathotypes Pa-2 and Pa-3, and four standard cultivars, namely Saturna, KTT 60-21-19, ODV 22731 (the *S. vernei* hybrid GLKS 58.1642-4) and (VTN)^2 62-33-3, were inoculated with eleven *G. pallida* Pa-3 isolates in 1982, 1983 and 1984

Table 1

The resistant ancestors of the clones and standard varieties. The number per source refers to the number of times the ancestor was used as progenitor.

	Rank*	Source**								
Resistant clones		*a*	*b*	*c*	*d*	*e*	*f*	*g*	*h*	*i*
AM-66-182	1	2	1	—	—	—	—	—	—	—
AM-76-999	2	1	2	1	1	—	—	—	—	—
AM-74-605	3	—	1	1	—	—	—	—	—	—
AM-77-3169	4	3	3	2	1	—	—	—	—	—
AM-77-3061	5	4	3	1	—	—	—	—	—	—
AM-78-3813	6	1	1	—	—	—	—	1	—	—
AM-78-336	7	2	1	1	—	—	—	—	—	—
AM-78-3704	8	—	—	1	—	1	—	—	—	—
AM-78-3679	9	2	2	—	—	1	1	—	—	—
AM-78-4102	10	—	—	1	—	—	—	—	1	—
AM-78-3778	11	1	2	1	—	—	—	1	—	—
AM-78-3787	12	—	—	—	—	—	—	1	1	—
Standard										
Saturna	1	—	—	—	—	—	—	—	—	—
KTT 60-21-19	2	—	—	—	—	—	—	—	—	1
ODV 22731	3	—	1	—	—	—	—	—	—	—
(VTN)^2 62-33-3	4	1	1	—	—	—	—	—	—	—

* The rank is based in the resistance level within the group resistant clones or standards respectivily; 1 = the most susceptible clone or standard (see Tab. 3).
** The letter refers to the letter mentioned below.

Source   *Pedigree*
a.   *S. vernei* 24/20 = (V × CLB) = (CPC 2488-3 × 2487-3) × Ulsterknight
b.   *S. vernei* I-3 = (V4N × T × T) × sp. Schwalbe (796/84 × 5)
c.   *S. vernei* II sp. Schwalbe = V57.1386/53 × sp. Schwalbe
d.   Colch. 241-1 = *S. vernei* s. sp. *balsii* EBS 1984 × *S. stenotonum* WAC 780
e.   *S. vernei* LGU8 × (Grata × S. opl.) × *S. vernei* LGU8 × *S. spegazzini* 440
f.   B 3769 = (*S. Leptophyes* EBS 1044 p3 × *S. santa rosae* EBS 1778) × US W 197
g.   F 78 = *S. vernei* LGU8 × (Grata × S. opl.) × G.5586
h.   F 93 = (T2N × *S. vernei* 218-16) × (*S. vernei* LGU8 × T2N)
i.   *S. kurtzianum* 54

(Tabs 1 and 2). The four standard cultivars are the differentials used for the identification of the *G. rostochiensis* and *G. pallida* virulence groups (Kort *et al.,* 1977).

Each year 33 sprouted tubers per plant genotype were planted in separate clay pots of 10 cm dia. The experiment was laid in a factorial randomized block design with three replicates (one replicate per year) of 16 × 11 treatments. The pots were filled with loam sand and inoculated with a Pa-3 isolate, 30 cysts per pot, three pots per isolate per plant genotype. The *G. pallida* isolates were multiplied in 1979 and 1983 on the susceptible cultivar Maritta and stored at 4. The average (hatched) larvae per cyst of the initial inoculum is given in Table 2.

Table 2

Name, origin, year of isolation and viability of *Globodera pallida* Pa-3 isolates.

Name	*Origin*	*Province*	*year*	*viability*[1]
Rookmaker	Valthe	Drente	—	466
Coll. 1077	Oostdonge-radeel	Friesland	—	346
Coll. 1112	Westerbork	Drente	—	432
A75-126-23	Borger	Drente	1975	376
A75-250-39	Gasselte	Drente	1975	177
A75-884-4	Vriezenveen	Overijssel	1975	212
A76-1013-1	Zweeloo	Drente	1976	163
A76-126-4	Borger	Drente	1976	206
A78-1003-3	Zuidwolde	Drente	1978	216
A78-775-3	Smilde	Drente	1978	147
A78-924-5	Westerbork	Drente	1978	41
E'83[2]	—	—	1983	120[2]

(1) The average number of hatched larvae per cyst in 1980 (or 1984 for E' 83).
(2) E' 83 is a mixture of 7 different isolates, multiplied in 1983 on Maritta.

The growing conditions, soil temperature and soil moisture control, were as described by van der Wal and Vinke (1982). The water supply was stopped eight weeks after planting. When the soil was air-dry, the cysts were recovered by flotation and their numbers determined.

To make the means and variances independent and the variance stable, square root transformation was applied to the data before analysis of variance was undertaken using the statistical programme GENSTAT (Nelder, 1977).

In a second experiment carried out in 1985 and 1986 the effect of plant genotype on the numbers of viable juveniles per cyst was tested. Cysts of four *Globodera pallida* Pa-3 isolates, Coll. 1077, Rookmaker, A 78-775-3 and E'83, were produced on pot-grown plants of Maritta, Saturna, KTT 60-21-19, ODV 22731 (VTN)^2 62-33-3 and AM 78-3778. The experiment was laid out

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in a randomized block design with three replicates (one plant per replicate). The nematode inoculation, the growing conditions and the recovering of the cysts were the same as in the first experiment. Cysts were stored after air-drying at 20° for sixteen weeks until the start of hatching. Larvae were hatched from dry cysts as decribed by Janzen (1968).

One batch of 50 cysts per plant, taken at random, was soaked on a nematode filter in one ml. solution of flavianic acid (0.1 gram per liter) for four days at 20° before juveniles were stimulated to hatch by replacing the flavianic acid solution with one ml. potato root diffusate (PRD). For the PRD solution dried PRD powder obtained from the Plant Protection Service in Wageningen, was solved in water, 12 mg per liter. At intervals of three and four days, cysts were placed alternately in fresh flavianic acid solution and PRD respectively, and the solution with the hatched juveniles was collected and stored at 4°. After six weeks the solution with the hatched juveniles was diluted with water to 100 ml, and the number of larvae was assessed per ml in four-fold replication.

Results and discussion

Compared with the standard cultivars the reproduction rate of the *G. pallida* Pa-3 isolates is significantly less on the selected resistant clones (Tab. 3). The average square root of the number of cysts of the resistant clones varies from 4.8 to 7.0, whereas for the standard cultivars the average varies from 10.7 for $(VTN)^2$ 62-33-3 to 22.8 for Saturna.

Because the number of cysts on the standard cultivars was considerably larger than that on the selected resistant clones the standard deviations based on the pooled error mean square are too large for comparison among resistant clones and fail to detect useful differences. Therefore, the data was subdivided and analysed separately. The results are summarized in the Tables 3, 4 and 5.

The analyse of variance of the data from the resistant clones demonstrated significance for the effects of plant genotype (A) (F = 42.43, d.f. 11 and 220; s.e. × = 0.17; LSD 5 % = 0.48); Pa-3 isolate (B) (F = 11.08, d.f. 10 and 220; s.e. × = 0.18; LSD 5 % = 0.50) and year (C) (F = 19.07, d.f. 2 and 220; s.e. × = 0.35; LSD 5 % = 0.98). Besides a small but significant effect was observed for the interactions AB (F = 1.99), BC (F = 4.30) and AC (F = 3.23).

Also for the data of the standard cultivars significance for the effect of plant genotype (F = 72.69, d.f. 3 and 60; s.e. × = 1.78; LSD 5 % = 5.04), Pa-3 isolate (F = 2.42, d.f. 10 and 60; s.e. × = 1.08; LSD 5 % = 3.04) and year (F = 17.14, d.f. 2 and 60; s.e. × = 2.06; LSD 5 % = 5.82) was observed as well as a small but significant effect for the interactions (F_{AB} = 1.84; F_{BC} = 4.36; F_{AC} = 3.23). Thus the differences

Table 3

Test matrix showing the year effect (a) on *Globodera pallida* Pa-3 cysts formed on the resistant clones and the standard cultivars.

Plant genotype	Year			Mean (b)
	1	2	3	
Resistant clones				
AM 66-182	6.9	6.3	7.7	7.0
AM 76-999	6.0	5.7	6.8	6.2
AM 74-605	6.2	5.4	6.0	5.9
AM 77-3169	6.1	5.9	5.5	5.8
AM 77-3061	5.9	5.1	5.6	5.5
AM 78-3813	5.6	5.0	4.9	5.1
AM 76-336	5.3	5.0	4.9	5.1
AM 78-3704	5.2	4.9	4.8	4.9
AM 78-3679	5.0	4.9	4.9	4.9
AM 78-4102	5.3	4.7	4.6	4.8
AM 78-3778	5.2	4.7	4.6	4.8
AM 78-3787	5.0	4.6	4.8	4.8
Mean (c)	5.6	5.2	5.4	5.4
Standard				
Saturna	26.3	17.0	25.2	22.8
KTT 60-21-19	20.1	17.0	19.4	18.8
ODV 22731	15.3	12.7	14.7	14.2
$(VTN)^2$ 62-33-3	11.9	9.8	10.5	10.7
Mean (d)	18.4	14.2	17.5	16.7

(a) expressed as the average of the square root of the number of cysts (pooled data from all isolates)
(b) s.e. × AM clones = 0.17, LSD 5 % = 0.48
   s.e. × standard CV's = 1.78, LSD 5 % = 5.04
(c) s.e. × year = 0.35, LSD 5 % = 0.98
(d) s.e. × year = 2.06, LDS 5 % = 5.82

in responses of the plant genotypes vary with the virulence of the Pa-3 isolate and the year, and the differences in virulence of the Pa-3 isolates vary with the year too. In the Tables 3 and 4 the year effects on the plant genotype and isolate responses are shown. It is clear that in general the nematode isolates developed well in the first and third year, especially on the standard varieties and less in the second experimental year. Because the inoculum in 1982 and 1983 was produced in 1979 and that in 1984 was produced in 1983, the year effect might be due to a reduction in viability during storage of the cysts. However, the isolate A 75-250-39 seems less affected by the year influence. With plant genotypes homozygous for the resistance genes and with " Pa-3 " isolates homozygous for the virulence genes no interaction between plant genotype and isolate is expected and differences in development are explained by differences in fitness or agressiveness between isolates. The plant genotype × isolate interaction within the group of

Table 4

. Test matrix showing the year effect (a) on *Globodera pallida* Pa-3 isolates on resistant clones (I) and standard varieties (II).

Isolates	Year (I)				Year (II)			
	1	2	3	Mean (b)	1	2	3	Mean (c)
Rookmaker	6.4	5.8	6.3	6.2	21.4	11.9	17.6	17.0
A 75-250-39	5.5	6.1	6.0	5.9	14.8	15.1	16.1	15.3
A 76-126-4	5.5	5.5	5.6	5.5	15.2	12.7	20.1	16.0
Coll. 1112	5.7	4.8	5.9	5.5	18.7	10.4	19.5	16.2
A 75-126-3	5.4	5.6	5.1	5.4	17.8	21.1	13.1	17.3
A 75-884-4	5.8	4.9	5.3	5.3	19.0	15.6	17.4	17.4
A 76-1013-1	5.3	5.0	5.6	5.3	9.7	13.8	16.0	13.2
A 78-1003-3	5.5	5.1	5.0	5.2	15.8	13.3	20.6	16.6
Coll. 1077	5.5	4.6	5.3	5.1	24.0	18.8	16.9	19.3
A 78-775-3	5.5	4.9	4.9	5.1	23.5	8.8	17.4	16.6
A 78-924-5	5.9	4.6	4.7	5.1	24.0	14.0	17.2	18.4
Mean (d)	5.6	5.2	5.4	5.4	18.4	14.2	17.5	16.7

(a) expressed as the average of the square root of the number of cysts
   (pooled data from all AM clones (I) or standard CV's (II).
. (b) s.e. × isolates = 0.18, LSD 5 $^0/_0$ = 0.50
(c) s.e. × isolates = 1.08, LDS 5 $^0/_0$ = 3.04
(d) s.e. × year (I) = 0.35, LSD 5 % = 0.98
(e) s.e. × year (II) = 2.06, LSD 5 $^0/_0$ = 5.82

resistant clones and within the group of standard culti-vars suggests differences in " pathotype " specific resistant genes between the plant genotypes and differ-ences in virulence genes between the isolates. The sequence of the (average) virulence of the Pa-3 isolates on the standard varieties is different from the sequence on the (pooled average) virulence of the isolates on the resistant clones (Tab. 5). This may be due to a variation in the frequency of different virulence genes in the isolates and of different resistance genes in the plant genotypes. It is remarked that the virulence is not correlated with the initial inoculum density (Tab. 2).

To estimate the " isolate sensitivity " of a resistant clone or a standard variety, the general effect of each isolate is first evaluated as the mean of all AM clones and standards. Then the value of each genotype is plotted against the isolate mean. The slope of the regression line measures the " isolate sensitivity " of the genotype (Falconer, 1981).

Regression analysis of the plant resistance per geno-type (Y) on the Pa-3 isolates (X), characterized by the average virulence on the standard varieties and on the AM clones (X = Vn = average square root of number of cysts per plant), shows significant regression coef-ficients for the standard varieties Saturna (p < 0.01) and ODV 2 2731 (0.01 < p < 0.05) and for a number of AM clones (p < 0.01) (Tab. 6). Therefore these plant geno-types are responsible for the observed plant genotype × isolate interaction (Figs 1 and 2). The AM clones can

be distinguished into two groups. One group with a significant regression coefficient b varying from 1.3 to 3.4 (s.e. = 0.31; T = b/s.e. varies from 6.74 to 10.87), meaning that the resistant level decreases on average by 1.3 to 3.4 units per " unit of virulence ", and one groupe with no correlation (b varying from — 0.6 to + 0.5), between the resistant levels of the plant genotypes and the average virulence level of the Pa-3 isolates (Figs 2 and 3). The most resistant plant genotypes belonged to this last group. Also for the standard varieties KTT 60-21-19 and (VTN^2) 62-33-3 there was no correlation between the resistance levels of the varieties and the average virulence level of the isolates.

In addition to the relative number of cysts, the number of viable juveniles per cyst is an important factor for the reduction of the nematode population. There-fore, in a separate experiment (experiment 2) the hatch-ing characteristics of cysts from four Pa-3 isolates produced on six different plant genotypes were studied. The results are summarized in Table 7. The analysis of variance showed a significant effect to the plant geno-type and the Pa-3 isolate on the hatching characteristics of the cyst populations produced (p < 0.001). The lowest number of second stage juveniles was obtained from Pa-3 isolate Coll. 1077 cysts and from cysts produced on AM 78-3778.

There are several hypotheses for the significant effect of the Pa-3 isolates. Because the potato cyst nematode reproduces through cross fertilization, the significant

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Table 5

Test matrix, showing the resistance spectra to *G. pallida* Pa-3 isolates of resistant clones
and standard cultivars and the virulence spectra of the Pa-3 isolates expressed as the average
of the square root of the number of cysts ($\sqrt{n}$) (pooled data from 1982, 1983, and 1984).

Plant genotype	Pa-3 isolates											
	Rook-maker	A 75 250-39	A 76 126-4	Coll. 1112	A 75 126-23	A 75 884-4	A 76 1013-1	A 78 1003-3	Coll. 1077	A 78 775-3	A 78 924-5	Mean (a)
Resistant clones												
AM 66-182	9.4	8.3	7.7	8.0	6.9	6.4	6.6	5.7	6.2	6.1	5.7	7.0
AM 76-999	7.0	8.2	5.8	5.6	7.3	5.8	6.5	6.0	5.1	5.2	5.4	6.2
AM 74-605	7.1	6.3	6.3	6.0	5.8	6.4	5.4	5.8	5.1	5.5	5.0	5.9
AM 77-3169	7.0	6.0	6.4	5.6	5.8	5.5	5.8	5.7	5.5	5.3	5.6	5.8
AM 77-3061	7.1	6.7	5.3	5.7	5.1	5.5	5.5	5.2	5.0	4.8	4.9	5.5
AM 78-3813	5.7	4.9	5.4	5.1	4.9	5.2	5.2	5.2	5.4	5.0	4.7	5.1
AM 76-336	5.4	5.2	4.9	4.9	5.2	5.3	4.7	5.3	5.0	5.2	4.8	5.1
AM 78-3704	5.2	4.8	5.3	5.1	4.7	5.3	4.8	4.6	5.0	5.1	5.0	4.9
AM 78-3679	5.3	5.3	4.7	5.0	4.6	4.8	4.9	5.0	4.9	4.6	5.0	4.9
AM 78-4102	5.1	5.3	4.5	5.0	4.9	5.1	4.9	4.6	4.5	4.9	4.5	4.8
AM 78-3778	4.5	4.4	5.0	4.8	4.6	4.6	4.8	4.8	5.3	4.8	5.2	4.8
AM 78-3787	5.1	4.9	4.9	4.9	4.7	4.5	4.6	4.7	4.8	4.7	5.1	4.8
Mean (b)	6.2	5.9	5.5	5.5	5.4	5.3	5.3	5.2	5.1	5.1	5.1	5.4
Standard												
Saturna	22.9	19.9	22.7	26.1	21.1	26.4	12.2	22.2	27.3	21.0	29.7	22.8
KTT 60-21-19	21.2	15.9	17.6	15.0	22.0	18.9	18.6	19.8	22.1	20.2	16.2	18.8
ODV 22731	12.5	13.0	13.1	13.8	13.9	13.6	11.2	13.9	18.3	15.4	18.0	14.2
(VTN)² 62-33-3	11.4	12.5	10.5	10.0	12.3	10.8	10.8	10.4	9.7	9.8	9.8	10.7
Mean (c)	17.0	15.3	16.0	16.2	17.3	17.4	13.2	16.6	19.3	16.6	18.4	16.7

(a) s.e. × AM clones = 0.17, LSD 5 % = 0.48; s.e. × standard CV's = 1.78; LSD 5 % = 5.04
(b) s.e. × isolates = 0.18; LSD 5 % = 0.50
(c) s.e. × isolates = 1.08; LSD 5 % = 3.04

effect of the Pa-3 isolates may be based on variation in the frequency of virulence genes in the isolates; isolates with a high frequency of respectively pathotype Ro-1, 4, Ro-2, 3, Pa-2 or Pa-3, being more virulent on respectively the Ro-1, 4, Ro-2, 3, Pa-2 or Pa-3 susceptible cultivars. However differences in (minor) virulence genes and the occurrence of various resistance mechanisms may also affect the overall virulence of the isolates (Turner, Stone & Perry, 1983; Parlevliet, 1985; Stone, 1985).

The interaction between the resistant AM clones and Pa-3 isolates indicates differences in number and relative frequencies of " Pa-3 " virulence genes between isolates and differences in " Pa-3 " resistance genes between plant genotypes. The Pa-3 isolates therefore cannot be regarded as one Pa-3 pathotype in the strict sense, but rather as a virulence group composed of individuals carrying different virulence genes and inter alia virulence genes to break through the Pa-2 resistance in (VTN²) 62-33-3. The difference in resistance ×

isolate interaction between the AM clones suggests at least two " Pa-3 " virulence genes and two corresponding resistance genes present in this material.

The significant effect of the plant genotype may be due to differences in number or the origin of the resistance genes. The most resistant clones all have *S. vernei* LGU8 in their ancestry (Tab. 1). However, owing to the complex of resistance genes in the progenitors of the clones and the absence of genetic analysis, this hypothesis could not be tested in this experiment.

Electrophoretic analysis of the protein composition of the various Pa-3 isolates showed large differences, suggesting differences for a large number of genes (Bakker, pers. comm.). For genetic analysis of " virulence " and the effect of minor genes influencing the fitness of different Pa-3 populations, Pa-3 genotypes which are homozygous for virulence should be available.

Conclusions

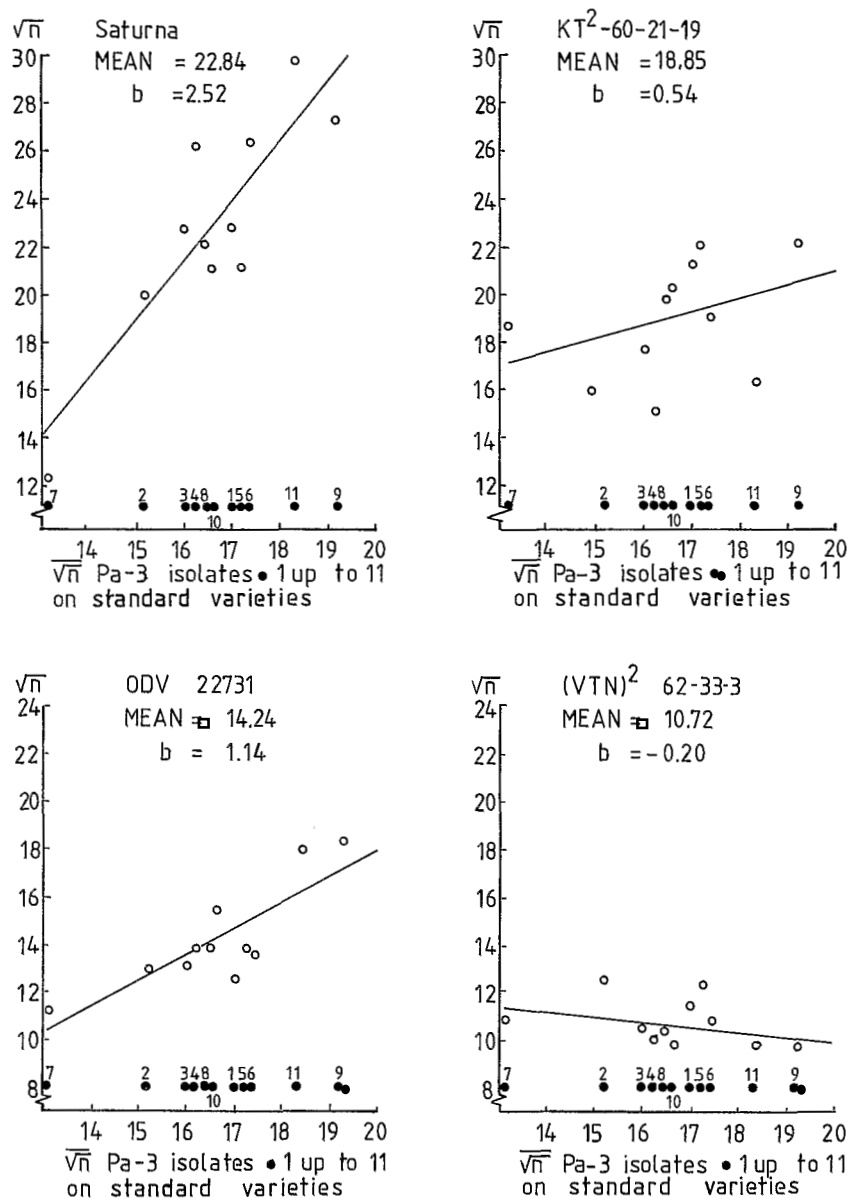There is variation in the level of resistance of the Pa-3

Fig. 1. The resistant level (Y) of the standard cultivars Saturna, KTT 60-21-19, ODV 22731 and (VTN)² 62-33-3 for the Pa-3 isolates, characterized by the average virulence Vn (n = number of cysts per plant) on the standard varieties. Y = the average Vn per Pa-3 isolate.
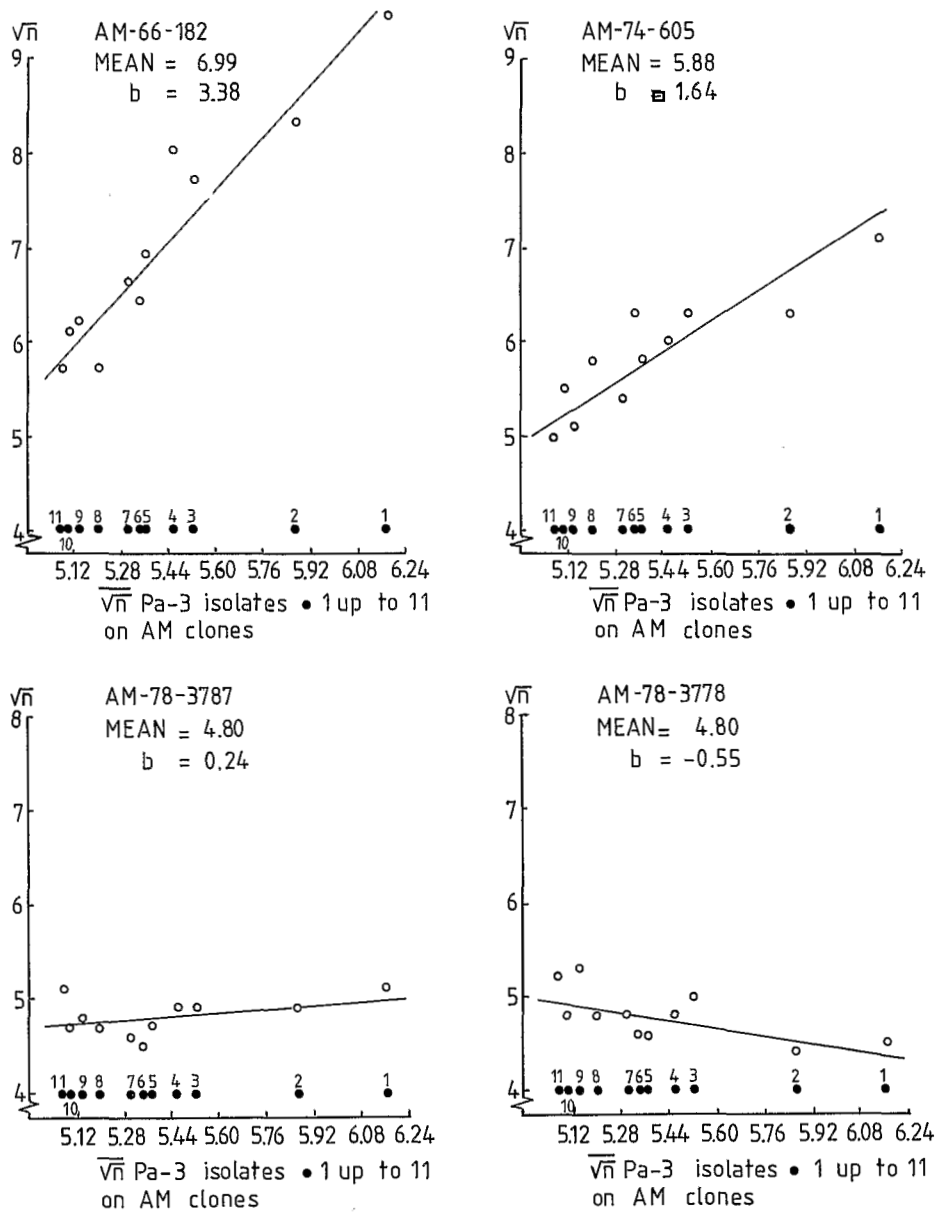
Fig. 2. The resistant level (Y) of the plant genotypes AM 66-182; AM 74-605; AM 78-3787 and AM 78-3778 for the Pa-3 isolates characterized by the average virulence Vn (n = number of cysts) on the resistant clones. Y = average of Vn per Pa-3 isolate.

Table 6

The regression coefficients (b) of the regression lines
of the resistant level of the standard cultivars (I)
and the resistant clones (II) on the Pa-3 isolates[1].

Genotype	Estimate b	S.E.	T[2]
I Standard			
Saturna	2.5	0.38	6.64**
KTT 60-21-19	0.5	0.38	1.43
ODV 22731	1.1	0.38	3.01*
(VTN)² 62-33-3	− 0.2	0.38	− 0.53
II Clones			
AM 66-182	3.4	0.31	10.87**
AM 76-999	2.0	0.31	6.49**
AM 74-605	1.6	0.31	5.28**
AM 77-3169	1.3	0.31	4.01**
AM 77-3061	2.1	0.31	6.74**
AM 78-3813	0.4	0.31	1.39
AM78-336	0.3	0.31	0.86
AM 78-3704	0.2	0.31	0.67
AM 78-3679	0.5	0.31	1.58
AM 78-4102	0.5	0.31	1.72
AM 78-3778	− 0.6	0.31	− 1.78
AM 78-3787	0.2	0.31	0.78

(1) Pa-3 isolates are characterized by the average virulence level; I) on the standard cultivars and II) on the resistant clones.
(2) T = b s.e. : *significant for $0.01 < p < 0.05$; **significant for $p < 0.01$

resistant potato clones to *G. pallida* Pa-3 isolates. However, this variation partly depends on the virulence of the Pa-3 isolates. In the initial screening for resistance, assessment of the resistance can be based on the screening to the Pa-3 isolate Rookmaker. Because with this isolate the clones with different (average) resistance level are distinguished. To differentiate between resistant

clones, the clones should be tested during some years with a representative sample of Pa-3 isolates separately, for instance with Rookmaker, Coll. 1112 and Coll. 1077. Besides, in addition to the selection based on the number of cysts produced, the average number of second stage juveniles per cysts should be taken into account as well. Based on the results of this experiment the resistant clone, AM 78-3778, is selected to identify " new " virulence groups of *G. pallida*.
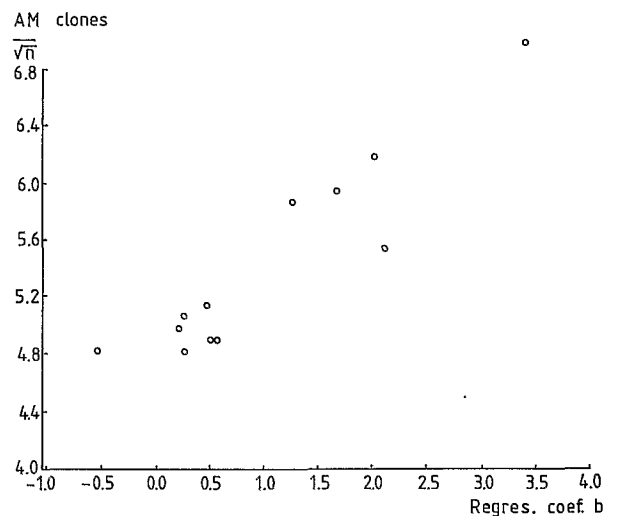

Fig. 3. The relation between b and the average resistant level of the $Y = \sqrt{n}$ per genotype; n = number of cysts per plant. X = b = the " slope " of the regression of the plant resistance on the Pa-3 isolates (S.E. (b) = 0.31).

Table 7

The number[1] of hatched second stage juveniles from cysts of four Pa-3 isolates
produced on six different potato cultivars.

Pa-3 isolates	Cultivars						
	Maritta	Saturna	KTT 60-21-19	ODV 22731	(VTN)² 62-33-3	AM 78-3778	Average[2]
Coll. 1077	87.1	66.3	65.9	34.5	42.8	5.0	50.3
E' 83	105.8	157.6	75.2	71.9	78.7	43.0	84.6
Rookmaker	100.8	105.0	86.0	85.9	110.5	52.2	90.3
A 78-775-3	133.1	101.9	85.8	79.4	106.5	19.3	87.7
Average[2]	106.7	103.2	77.5	67.9	84.6	29.9	78.0

(1) The average number of juveniles per ml sample from 100 ml solution of hatched juveniles from 50 cysts.
(2) The ANOVA demonstrated a highly significant effect of plantgenotype ($F = 22.7$, d.f. 5 and 46; s.e. $\times = 8.24$; LSD 5 % = 23.5) and of Pa-3 isolate ($F = 15.44$, d.f. 3 and 46; s.e. $\times = 10.09$; LSD 5 % = 28.7).

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