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The effect of physiological age of potato tubers on female production of potato cyst nematodes (*Globodera pallida* Pa 2/3)

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Abstract

Fourteen cultivars generally regarded as uniformly susceptible to *Globodera pallida* Pa 2/3 were assessed in plastic closed containers for degree of susceptibility and also for root and sprouting characteristics. The material was assessed by scoring degree of sprouting before planting and number of cysts and root growth at the end of experiment at intervals from the time of initial dormancy break through to prolific sprouting. Using covariate analyses, it was found that the degree of root development, particularly in the earlier assessments, significantly influenced the degree of cyst development and so the perceived levels of susceptibility/resistance. Having taken account of root growth characters,significant differences between the cultivars with regard to nematode multiplication were still evident. The implications of the results are discussed in relation to potato breeding and nematological studies.

Introduction

Resistance to the potato cyst nematode,*Globodera pallida* (Stone) has been identified and transferred to *Solanum tuberosum* from a number of wild and semi-cultivated sources. The most frequently utilized include *S. tuberosum* ssp. *andigena* (Juz. et Buk.), *S. vernei* (Bitt. et Wittm.) and *S. spegazzinii* (Bitt.) [Ross, 1986]. Low levels of resistance, or differences in the degree of susceptibility, have been reported with *S. tuberosum* ssp. *tuberosum L.* Gemmell [1943] found that the cultivars 'Epicure' and 'Doon Star' produced fewer and smaller cysts than 'Golden Wonder' and 'Majestic'. However, O'Brien and Prentice [1931] described 'Epicure' as extremely susceptible. More recently, Dale and Phillips [1985] and Arntzen and Bakker [1988] identified considerable differences between a range of susceptible cultivars with regard to the number of cysts formed. The latter authors found that the extent of the differences between susceptible cultivars varied with different nematode species, different pathotypes and, to a lesser extent, with different populations of the same pathotype. Phillips and Dale [1982] and Dale and Phillips [1985] also identified a heritable component to the observed variation between cultivars previously regarded as equally susceptible.

The current study re-examined a range of cultivars within *S. tuberosum* ssp. *tuberosum* described as susceptible. These are evaluated over a range of physiological stages. The objective of the approach was to more closely define or explain some of the observed, and also previously reported, variation.

Materials and methods

Seed tubers derived from a common source of fourteen cultivars generally regarded as susceptible to *G. pallida* (Pa2/Pa3, Lindley) plus two cultivars with partial resistance, were tested by using transparent plastic closed containers (240 mls) following the method described by Phillips et al. [1980] with an inoculum level of 3,500 eggs

per container. For each cultivar, six small tubers per assessment were planted in six individual containers and placed, randomised, in replicated blocks in trays at 20 °C. The experiment consisted of seven assessments, each organised as described previously but planted and subsequently inoculated at 3 week intervals sequentially with the first assessment set up at the initial visible signs of dormancy break. The numbers of cysts formed, visible through the transparent walls of the containers, were counted at the end of each assessment, between 56 and 63 days. The dates of setting up the different assessments are given in Table 1.

The degree of sprouting at the start of each assessment was visually scored on a 1 to 9 scale, with 1 indicating prolific sprouting and 9 no visible sprouting over 3 mm long. Root development at the end of the test was scored visually on a 1 to 9 scale, with 1 indicating very good root growth and 9 indicating very poor or negligible root growth.

Table 1. Dates of initiation and assessment of PCN susceptibility during course of experiment

Time	Date initiated and sprouting assessed	Date cyst counted and root growth assessed
1	20 December	21 February
2	10 January	13 March (lost due to contamination)
3	31 January	3 April
4	21 February	20 April
5	13 March	8 May
6	3 April	29 May
7	27 April	22 June

Results

The container tests were successful in all but the second group of plants to be set up (see Table 1), which had to be discontinued due to fungal contamination. The two control cultivars with known partial resistance to *G. pallida* Pa2/3 derived from *S. vernei* (cv. Morag) and *S. tuberosum* ssp. *andigena* (cv. Eden) performed as expected, with cv. Eden being consistently more resistant than cv. Morag. While the results of these two cultivars are included in the tables summarising the results, they were subsequently excluded from the more detailed analyses which examined differences in the susceptible genotypes. They were included as controls to ensure the container tests were suitable for assessing PCN reproduction over a wide range of host susceptibilities.

The summary analyses of the individual variates: number of cysts (square root transformation), sprout and root development are presented in Table 2. The major effects of cultivar and time, and the appropriate interactions were significant for all three variates. The mean cyst numbers and the ranks of the cultivars within the different assessment dates are given in Table 3 and the mean sprout data and root development data in Tables 4 and 5 respectively. The differences between the cultivars and between the treatments for the three variates are largely as expected, with the degree of sprouting (Table 4) increasing from date 1 through to the later date 7. The root growth in the earlier assessments was markedly less than in the later assessments. Notable for poor root growth (Table 5) are the cultivars cv. Maris Bard (4.6) and cv. Home Guard (4.9), which are both described as first early maturity, and cv. Pentland

Table 2. Analyses of individual variates, including cyst number (square root transformation), sprout development and subsequent root development assessed at end of tests

		MS	MS	MS
	df	Square root cysts	Sprout development	Root development
Cultivar	13	11.22***	51.62***	26.87***
Time	5	79.35***	138.86***	47.98***
Cultivar × time	65	7.88***	2.28**	2.77***
Residual	420	4.05	1.48	1.38

**0.01 < P < 0.01; ***P < 0.001

Table 3. Susceptibility of potato cultivars in plastic closed containers. Cultivars ranked according to mean susceptibility. Figures given are mean number of cysts on rootballs (6 replicates)

Cultivar	Maturity class	Time 1	3	4	5	6	7	Mean
P. Javelin	1	53.7	98.3	78.8	57.8	83.0	72.5	74.0
Estima	2	28.8	80.0	81.5	60.7	65.0	76.4	65.4
P. Dell	3	50.7	47.7	57.0	63.3	80.0	82.8	63.6
Desiree	3	10.0	100.7	60.7	71.3	67.4	71.4	63.3
P. Squire	3	32.3	62.5	52.8	58.0	89.7	76.5	62.0
M. Piper	3	31.7	38.7	85.2	66.0	68.8	78.2	61.4
Record	3	34.0	47.5	74.3	51.3	93.8	62.3	60.5
M. Bard	1	29.3	48.7	49.2	61.2	77.2	87.2	58.8
Wilja	2	48.0	62.0	48.5	55.2	59.7	73.5	57.8
Baillie	2	19.2	67.8	63.5	54.0	72.8	43.2	53.4
Cara	3	44.3	66.5	37.7	39.7	65.3	43.8	49.6
Home Guard	1	50.2	65.0	51.6	40.2	41.4	46.4	49.1
King Edward	3	36.8	59.0	22.2	34.3	71.3	70.6	49.0
P. Crown	3	46.7	45.4	50.2	46.8	47.6	40.8	46.2
Means		36.8	63.6	58.1	54.3	70.2	66.1	58.2
s.e.d.	Cultivar	6.16	Treatment	4.04	Cultivar.treatment			15.10
Morag	3	9.7	25.0	21.5	24.0	29.0	45.8	25.8
Eden	3	4.0	8.3	12.2	7.8	15.7	14.8	10.6

Table 4. Mean values (6 replicated) of the degree of sprouting when individual dates were inoculated. Scored on a 1 (prolific sprouting) to 9 (no sprouting) scale

Cultivar	Time 1	3	4	5	6	7	Mean
P. Javelin	6.7	5.7	6.2	3.3	3.8	3.3	4.8
Estima	9.0	7.2	6.9	5.7	5.2	5.2	6.5
P. Dell	8.4	6.8	7.2	6.2	5.2	5.0	6.5
Desiree	9.0	6.9	6.8	6.2	5.2	4.2	6.4
P. Squire	8.5	6.6	4.9	5.3	4.0	4.6	5.7
M. Piper	7.3	6.8	5.1	4.8	4.2	3.6	5.3
Record	7.5	6.1	6.3	6.5	5.7	5.5	6.3
M. Bard	8.3	7.1	7.2	5.8	4.5	5.5	6.4
Wilja	6.3	4.4	5.1	4.8	2.9	2.7	4.4
Baillie	8.4	7.3	7.4	7.2	6.0	6.2	7.1
Cara	7.5	6.4	6.3	4.8	4.1	3.7	5.5
H. Guard	6.0	3.2	2.2	1.4	1.2	1.0	2.5
K. Edward	5.6	6.4	4.3	3.2	4.7	4.6	4.8
P. Crown	8.5	7.2	6.6	5.5	4.9	4.6	6.2
Mean	7.6	6.3	5.9	5.0	4.4	4.3	5.6
s.e.d.	Cultivar	0.29	Treatment	0.17	Cultivar.treatment		0.70
Morag	8.2	5.1	3.8	3.7	2.0	2.0	4.0
Eden	8.6	6.8	6.3	5.3	6.1	5.3	6.4

Table 5. Mean value (6 replicates) of root development at end of each assessment for 16 cultivars. Scored on a 1 (good growth) to 9 (poor growth) scale

	Treatment						
Cultivar	1	3	4	5	6	7	Mean
P. Javelin	4.3	2.2	2.0	2.7	2.4	2.2	2.6
Estima	4.3	2.7	2.9	2.8	2.5	2.4	2.9
P. Dell	5.3	5.8	3.0	5.2	4.2	3.2	4.5
Desiree	6.6	3.8	3.7	2.8	3.8	3.0	4.0
P. Squire	5.9	2.3	2.8	2.6	2.3	3.0	3.1
M. Piper	5.8	3.5	3.0	2.7	2.7	3.0	3.4
Record	4.2	5.2	2.7	2.7	2.6	2.8	3.4
M. Bard	6.5	4.5	3.9	4.3	4.5	3.8	4.6
Wilja	4.6	4.3	2.9	3.9	3.8	2.7	3.7
Baillie	4.8	1.7	2.6	1.7	1.0	2.4	2.3
Cara	4.1	1.8	2.3	2.7	2.0	2.4	2.5
H. Guard	4.8	4.5	4.7	6.0	5.2	4.2	4.9
K. Edward	4.1	2.3	2.3	1.8	2.2	2.4	2.5
P.Crown	4.6	3.2	1.8	1.6	1.4	2.0	2.4
Mean	5.0	3.4	2.9	3.1	2.9	2.8	3.3
s.e.d	Cultivar	0.28	Treatment	0.18	Cultivar.treatment		0.68
Morag	4.6	2.2	2.9	1.7	1.5	2.9	2.6
Eden	4.6	5.2	3.0	4.2	4.8	2.8	4.6

Dell, which is known to have a relatively small root system. Cultivars such as Pentland Crown and particularly Cara, are known to have large root systems.

Of particular interest in the present study, however, was how the degree of sprouting or root development of the material affected the assessment of susceptibility to PCN. The observed variation was therefore re-examined using root development and degree of sprouting as covariates. The data were partitioned according to cultivar and maturity rating given in Table 3a, and the summary analysis in Table 6. The covariate analysis demonstrates that the degree of root development accounts for a significant part of the observed variation in cyst number, although significant differences were still identified between the potato cultivars and between the different dates of assessment. The mean cyst data (Table 7a) are adjusted for the covariates. The covariate analyses examining the effect of partitioning the data according to maturity indicated that, while maturity played a significant role with respect to sprout and root development, it did not appear to influence significantly the development of cysts.

Table 6. Covariate analysis of square root of cyst data, using root development and degree of sprouting as covariates

Item	df	MS
Cultivar	13	17.89***
Time	5	17.61***
Cultivar & time	65	6.16***
Covariates	2	94.39***
Residual	418	3.58
Covariate regression		
Covariate	Coefficient	s.e.
roots	–0.592	0.0819
sprouts	–0.027	0.0789

***P < 0.001

The correlation coefficients, based on the mean cyst counts, adjusted for the covariates across dates are presented in Table 7b. The earlier dates, when root development was poorest, demonstrated no agreement, with improved agreement between the later dated e.g. 4, 5, 6 and 7, when root growth

Table 7a. Susceptibility of potato cultivars to *G. pallida*, given as square root transformation of the number of cysts. Figures adjusted for covariates (Sprouts and roots). Figures are means of 6 replicates, cultivars ranked according to degree of susceptibility

		Time						
Cultivar	Maturity class	1	3	4	5	6	7	Mean
P. Dell	3	8.13	8.26	7.30	9.02	9.29	8.87	8.48
P. Javelin	1	7.56	9.19	8.05	7.09	8.36	7.71	8.00
M. Bard	1	6.49	7.42	6.59	8.31	9.28	9.39	7.91
Desiree	3	3.83	10.33	7.94	8.04	8.27	8.16	7.76
M. Piper	3	6.84	6.17	8.72	7.48	7.78	8.48	7.58
Wilja	2	7.60	8.31	6.38	7.51	7.43	8.06	7.55
Estima	2	5.37	8.42	8.55	7.36	7.48	8.07	7.54
Record	3	6.16	7.36	8.09	6.72	9.21	7.41	7.49
H. Guard	1	7.67	8.55	7.70	7.74	6.44	6.35	7.41
P. Squire	3	6.34	7.31	6.64	6.89	8.68	8.44	7.38
Cara	3	6.64	7.24	5.49	5.73	7.17	5.92	6.37
Baillie	2	4.23	7.24	6.82	5.94	7.08	5.97	6.21
P. Crown	3	7.55	6.64	6.06	5.67	5.35	5.41	6.11
K. Edward	3	5.76	6.99	3.85	4.58	6.88	7.59	5.94
Means		6.44	7.82	7.01	7.01	7.76	7.56	7.27
s.e.d.	Cultivar	0.477		Times	0.338	Cultivar.times		1.120

Table 7b. Correlation coefficients based on data in Table 7a

	Time 1	Time 3	Time 4	Times 5	Time 6
Time 3	–0.19				
Time 4	–0.03	0.36			
Time 5	0.23	0.50*	0.66***		
Time 6	–0.05	0.24	0.36	0.58*	
Time 7	0.03	0.22	0.28	0.64*	0.78***

*P < 0.05; ***P < 0.001

was better for all cultivars. Agreement clearly improved later in the study, being best between dates 5, 6 and 7.

Discussion

The present study confirms previous results which have identified both phenotypic and heritable differences in the levels of cyst production between *S. tuberosum* potato cultivars previously grouped as susceptible. Differences were also identified with regard to the degree of sprouting and root development within the tests. While there were significant differences between the cultivars when grouped by maturity (see Table 3) for sprout and root development (both $P < 0.001$), this effect of maturity was not evident with regard to development of cysts. From Tables 4 and 5 it would appear that the effect of maturity on these two characters was most marked within the first two or three assessment dates.

The covariate analysis indicated, as might be expected, that the degree of root growth significantly influences the number of cysts produced. Taking root development into consideration, the earlier dates would appear to be least reliable (see Table 7a, b) with good agreement between the later dates 5, 6 and 7. Most notable perhaps are the cultivars Pentland Dell and Maris Bard which

are both more susceptible (see Tables 3 and 7a) when root development is taken into account. Indeed, the former cultivar, classed as extremely susceptible, was originally described as relatively resistant, or less susceptible, when compared with other cultivars by Dale and Phillips [1985]. However, in a field situation, varieties such as P. Dell may suffer considerable yield losses [see Phillips et al., 1988] and, through having significantly smaller root systems may result in reduced nematode multiplication rates.

The present study has confirmed that differences do exist between cultivars previously classed as susceptible. The origin of such variation is not known. Dale and Phillips [1985] suggested that some of the variation has probably been introduced unintentionally from various wild species such as *S. acaule*, *S. demissum*, *S. phureja* and *S. stoloniferum* along with the transfer of other targeted traits such as blight and virus resistance. Some of the variation has undoubtedly been present undetected within the subspecies *tuberosum* since its introduction into Europe. Ross [1986], in an extensive review, described some 97 European cultivars carrying genes originally derived from 13 different wild species, with *S. andigena*, *S. demissum* and *S. phureja* appearing in the genetic background of most of the listed varieties. The present study identifies that the root growth characteristics can contribute significantly to the subsequent cyst development. This is as expected, given that the root is an important component of the environment which directly influences the life cycle of the nematode.

The implications of the results reported here have foremost importance for plant breeders, but also to nematologists. While the levels of variation are not high when compared to that derived from such species as *S. vernei*, they will nonetheless influence populations in the field situation. Such differences may, in part, explain some of the results observed in field trials [Phillips et al., 1988] for various susceptible control cultivars.

The testing or assessment of material, whether by breeders within a programme or by various statutory bodies, should take account of the physiological state of the material as this may affect the rate of root development and so the degree of cyst multiplication, particularly amongst material with variable dormancy break.

The observed variation may influence breeders more directly. There is clearly a heritable component amongst such material for this characteristic [Phillips and Dale, 1982; Dale and Phillips, 1985; Delaert et al., 1988] and, as such, it may be a worthwhile objective for potato breeders. However, it would be prudent to ensure that other characters such as root size or rate of development are not adversely affected when attempting to isolate and increase levels of such resistance within *S. tuberosum*.

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