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The importance of wild potato species resistant to the potato cyst nematode, *Globodera pallida*, pathotypes P_4A and P_5A, in potato breeding. I. Resistance studies

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Summary

Seven wild diploid potato species, Series Tuberosa, representing 1023 clones were screened for resistance to the potato cyst nematode, *Globodera pallida.* Over 25% of the clones were resistant to pathotype P_4A and almost 30% were resistant to pathotype P_5A. The resistance in hybrid progenies of these and other resistant species with cultivated potatoes was evaluated, and over 2200 seedlings were screened. High frequencies of resistance (>50%) to P_4A were found in progenies with *Solanum leptophyes, S. vernei, S. gourlayi* and *S. capsicibaccatum,* whereas resistance to P_5A was found in these species as well as *S. sparsipilum.* The importance of nematode resistant wild species for potato breeding is discussed.

Introduction

The potato cyst nematodes *Globodera rostochiensis* Woll. and *G. pallida* (Stone) Mulvey and Stone are important pests of the potato crop in many parts of the world. *G. pallida* is more common than *G. rostochiensis* in the Andean region of South America, and it may also be quite common now in most potato growing areas of the world (Scurrah & Franco, 1978).

Breeding varieties resistant to *G. rostochiensis* has been carried out for several decades, especially since the discovery of resistance in *Solanum vernei* and some clones of *S. tuberosum* ssp. *andigena* (Ellenby, 1948, 1952). In recent years however, there has been increased interest in obtaining potato varieties resistant to *G. pallida,* and there have also been associated studies on the biology of this species. The importance of genetic control of cyst nematodes in many developing countries needs no stressing, since small farmers in these countries commonly use little or no chemical control of these important pests. Consequently the identification of resistant germplasm and its effective utilisation in potato breeding has become one of the priorities of the International Potato Center.

Plant species with pest or disease resistance are often found where pests and diseases themselves are highly variable. Stone (1979) has indicated that the richest source of resistance genes to both *G. pallida* and *G. rostochiensis* is to be found in north-west Argentina. But although both these species appear to have originated in this region, Franco (1977) has suggested that scattered populations of *G. pallida* and *G. rostochiensis* became isolated during the Pleistocene glaciations and moved

northwards, with only *G. pallida* penetrating beyond Lake Titicaca (15° S). Consequently important sources of genetic resistance are to be found in Bolivia and in Peru. This has been confirmed by Soest et al. (1983a, 1983b), Male-Kayiwa (1983) and Wanyera (1984).

Dunnett (1960) was one of the first to screen extensively the large gene pool of tuber-bearing *Solanum* species for resistance to *G. rostochiensis*. He found resistance in *S. vernei, S. multidissectum, S. microdontum* and *S. megistacrobolum,* and emphasised their usefulness for breeding purposes. The resistance of *S. vernei* to potato cyst nematode has been extremely valuable, and it is effective against all pathotypes tested in Europe and the USA (Scurrah et al., 1973). It has been incorporated into the pedigrees of a number of Dutch and German varieties, principally conferring resistance to *G. rostochiensis* but also to some pathotypes of *G. pallida*. However, the search for better sources of genetic resistance must be continued. In this paper and another (Chavez et al., 1988a), an evaluation has been made of wild potato species for nematode resistance, the ease with which they can be crossed with cultivated potato species, and the resistance of hybrid progenies.

Materials and methods

Fifty-six accessions from seven wild potato species, representing 1023 clones from Series Tuberosa and 2239 seedligs representing 23 F1 families, within Series Tuberosa and between species within Series Tuberosa and other taxonomic series, were screened for resistance to *G. pallida,* pathotypes P_4A and P_5A, originating from Huancayo and Otuzco, Peru, respectively. The species used in this study, and name abbreviations are listed in Table 1.

Original accessions of wild species and hybrid families between resistant wild and susceptible cultivated species were grown from seedlings or tubers in the glasshouse, where the temperature varied between 15–20b° C. Tubers were used for the resistance evaluation of the wild species. Sprouted tubers were planted in 9cm clay pots filled with steam-sterilised compost. Three tubers of each clone were inoculated with 25 cysts each, one tuber receiving inoculum of pathotype P_4A, and the other two receiving P_5A.

Seedlings from the hybrid families were transplanted into individual 5cm plastic pots, four to five weeks after sowing. Each pot received an inoculum of 25 cysts of either P_4A or P_5A, and most progenies

Table 1. Tuber-bearing *Solanum* species used in this study.

Species	Abbreviation	Series	Ploidy	Status
S. brevicaule	brc	Tuberosa	2x	wild
S. canasense	can	Tuberosa	2x	wild
S. coelestipetalum	cop	Tuberosa	2x	wild
S. leptophyes	lph	Tuberosa	2x	wild
S. lignicaule	lgl	Tuberosa	2x	wild
S. microdontum	mcd	Tuberosa	2x	wild
S. multidissectum	mlt	Tuberosa	2x	wild
S. sparsipilum	spl	Tuberosa	2x	wild
S. vernei	vrn	Tuberosa	2x	wild
S. gourlayi	grl	Tuberosa	4x	wild
S. oplocense	opl	Tuberosa	6x	wild
S. capsicibaccatum	cap	Circaeifolia	2x	wild
S. commersonii	cmm	Commersoniana	2x	wild
S. papita	pta	Longipedicellata	4x	wild
S. goniocalyx	gon	Tuberosa	2x	cult.
S. phureja	phu	Tuberosa	2x	cult.
S. stenotomum	stn	Tuberosa	2x	cult.
S. tuberosum ssp. *andigena*	adg	Tuberosa	4x	cult.
S. tuberosum ssp. *tuberosum*	tbr	Tuberosa	4x, 2x	cult.

were tested for both pathotypes. One hundred seedlings each of selfed seed from the susceptible variety Renacimiento were inoculated with P_4A and P_5A as a control. Freshly tested viable inoculum, stored at 8° C was used in all screening experiments.

All pots were placed on benches where watering was carefully regulated by using fine sprinklers, especially in the first few weeks after inoculation while the juvenile nematodes were invading the roots. The final assessment of resistance was made seven to eight weeks after inoculation, and only those plants with a well-developed root system were evaluated. Plants were considered as resistant if the final cyst number on the root-ball surface was five or less, and as susceptible when six or more cysts were observed.

Results

Wild diploid species

The highest levels of resistance to both pathotypes were found in *S. brevicaule,* with a slightly higher resistance to P_4A (Table 2). At the other extreme was *S. coelestipetalum,* in which no resistance was found. About half the clones of *S. leptophyes* were resistant to both pathotypes. With *S. canasense, S. multidissectum* and *S. sparsipilum,* there were marked differences in reaction to the different pathotypes, with all three species manifesting a much higher level of resistance to P_5A. In contrast, *S. microdontum* showed much higher resistance to P_4A. The susceptible control variety Renacimiento had regularly more than 20 cysts on the root-ball surface of each plant in this replicated trial (three plants per pathotype).

F1 families

Twenty-two hybrid seedling families from interspecific crosses between resistant wild species and susceptible cultivated species and one intraspecific cross of *S. capsicibaccatum* were screened for nematode resistance. The results of the screening programme are given in Table 3.

In crosses within Series Tuberosa higher levels of resistance were found to P_5A than to P_4A except for progenies derived from *S. brevcaule, S. leptophyes* and *S. vernei.* Very high levels of resistance to P_5A (>80%) were found in progenies from crosses of *S. sparsipilum* with *S. goniocalyx* and *S. tuberosum* haploids. Even though the level of resistance to P_5A (as determined by percentage of clones resist-

Table 2. Percentage of clones resistant to *G. pallida* pathotypes P_4A and P_5A in seven diploid wild potatoes, Series Tuberosa.

Species	No. accessions screened	No. clones screened	% clones resistant to	
			P_4A	P_5A
S. brevicaule	6	61	98.3	91.8
S. canasense	7	53	18.8	30.1
S. coelestipetalum	1	40	0	0
S. leptophyes	4	65	55.3	41.5
S. microdontum	10	220	45.9	9.5
S. multidissectum	5	42	2.3	61.9
S. sparsipilum	23	542	10.1	29.3
	56[1]	1023[1]	25.7[2]	29.8[2]
cv. Renacimiento (control)	1	1	0	0

[1] Totals.
[2] Weighted means.

ant) in *S. sparsipilum* was not as high as in some of the other six species evaluated, all progenies derived from this species had good resistance to P_5A, and between 14 and 22% resistant to P_4A. The level of resistance in *S. microdontum* to both pathotypes was low. Although resistance to P_5A had been determined in *S. canasense*, this was not transferred to progeny from crosses with *S. stenotomum*.

Progenies from crosses between species previously identified as resistant at CIP were also evaluated. Hybrid derivatives of tetraploid *S. gourlayi* rated high resistance to P_4A, with >50% resistant in crosses with *S. tuberosum* ssp. *andigena*, and over 97% in crosses with ssp. *tuberosum*. Progenies from *S. oplocense* showed only a low level of resistance, less than 17%. About 30% of the seedlings

Table 3. Percentage of seedlings resistant to *G. pallida* pathotypes P_4A and P_5A in F1 seedling families.

Cross from which family derived	P_4A		P_5A	
	No. seedlings tested	% res.	No. seedlings tested	% res.
Tuberosa × *Tuberosa*				
(2x × 2x)[1]				
brc × gon	93	15.1	86	11.6
brc × 2x tbr	37	45.9	31	25.8
can × stn	–	–	51	0
lph × stn	24	25.0	14	21.4
lph × 2x tbr	53	58.4	52	40.4
mcd × phu	96	5.2	94	12.8
mcd × 2x tbr	92	3.3	91	2.2
mlt × phu	–	–	89	9.0
spl × gon	91	14.2	30	8.6
spl × phu	190	16.9	129	60.5
spl × stn	78	20.5	26	53.8
spl × 2x tbr	96	21.8	87	89.6
vrn × stn	21	52.3	20	25.0
vrn × 2x tbr	76	61.8	–	–
(4x × 4x)				
adg × grl	99	50.5	–	–
tbr × grl	42	97.6	–	–
(4x × 6x)				
tbr × opl	20	10.0	–	–
adg × opl	30	16.6	–	–
Longipedicellata × *Tuberosa*				
(4x × 2x)				
pta × 2x tbr	55	29.0	–	–
Circaeifolia × *other series*				
(2x × 2x)				
cap × cap[1]	29	100	24	100
cap × lgl[1]	17	100	17	100
(cap × lgl) × 2x tbr	41	29.0	71	14.0
cap × cmm	25	88.0	22	81.8
	1305[2]	25.9[3]	934[2]	28.9[3]
cv. Renacimiento selfed (control)	100	0	100	0

[1] Reciprocal crosses.
[2] Totals.
[3] Weighted means.

from crosses between *S. papita* (Series Longipedicellata) and *S. tuberosum* haploids were also resistant to P_4A. Both *S. gourlayi* and *S. oplocense* were susceptible to P_5A, and therefore progenies were not evaluated against this pathotype.

All seedlings from an intra-specific cross of *S. capsicibaccatum* (Series Circaeifolia) as well as the hybrid progeny from a cross with *S. lignicaule* (Series Tuberosa) were resistant to both P_4A and P_5A. However, this very high level of resistance was not transferred to hybrid progenies between these hybrids and *S. tuberosum* haploids. Progenies from a cross between *S. capsicibaccatum* and *S. commersonii* (Series Commersoniana) also had a high level of resistance. These progenies were originally developed for resistance to potato tuber moth, derived from *S. commersonii* (Chavez et al., 1988b).

Seedlings that had been obtained from selfed seeds of the variety Renacimiento were used as a control in this experiment. One hundred seedlings each were inoculated with pathotype P_4A and pathotype P_5A. Each seedling was susceptible with between six and more than 20 cysts per root-ball.

Discussion

The results of screening the seven wild diploid species from Series Tuberosa clearly demonstrates the broad genetic base for potato cyst nematode resistance in this wild germplasm from the central Andes of South America. This evidence adds considerable weight to the hypothesis of Franco (1977) and Stone (1979) concerning the evolutionary pathways of *G. pallida* and solanaceous species. Although most of the accessions from north west Argentina and southern Bolivia possess resistance to pathotypes P_4A and P_5A, there is no evidence to discard the possibility that these selected clones may also possess resistance to other pathotypes of *G. pallida* as may also be the case with their hybrid derivatives with cultivated species.

The direct transfer of cyst nematode resistance genes from wild diploid, tetraploid and hexaploid potato species into the cultivated gene-pool was possible with most of the species used, except *S. capsicibaccatum* and *S. lignicaule.* Hybrid populations of *S. sparsipilum* and *S. vernei* with cultivated diploid potatoes showed great intra-family variation with respect to the degree of resistance encountered. This broad variation can be explained in terms of either polygenic inheritance of resistance to *G. pallida* (Evans & Stone, 1977) or the variation of hatching controlled by the *S. vernei* genome in the hybrids (Williams, 1958); it might, however, be due to both of these factors. In addition variation of the hatching factor would severely influence the response of different plants to initial inoculation and therefore contribute to a modified expression of the resistance (Uhrig & Wenzel, 1981). The results obtained in this study, however, emphasise that the genes for resistance in the hexaploid *S. oplocense* and diploid *S. microdontum* have a rather low expression. The resistance of *S. vernei,* on the other hand, has been transmitted to nearly 50% and 30% of its progeny for P_4A and P_5A, respectively. The fact that distinction between resistant and susceptible clones is easier in progenies of *S. gourlayi* and the greater number of resistant clones was found in such progenies than in *S. vernei* is probably based on a simpler genetic basis of the resistance in the former species (Uhrig & Wenzel, 1981).

It is interesting to mention that some cultivars and advanced clones resistant to potato cyst nematodes have been developed which incorporate resistance genes from *S. vernei, S. multidissectum* and *S. tuberosum* ssp. *andigena.* The resistance that has been used in cultivars seems to be controlled to a large extent by only a few genes with major effects (Fuller & Howard, 1974). However, it has been pointed out that resistance does not last for ever, and sooner or later a source of resistance becomes less effective. Especially monogenic resistance can only be effective when there is a continuous influx of new resistance genes from various sources, and there must be the possibility of changing seed rapidly if a new pathotype becomes predominant in the population. Consequently, it is essential to have access to the genetic diversity of wild species.

In connection with the inheritance of resistance to the cyst nematode, the resistant/susceptible ratio found in the F1 progeny did not follow a predicted

ratio for a single dominant or recessive gene responsible for resistance. In addition to the complex genetic nature of the parental species used in wide crosses, in most cases only a small number of hybrids was obtained which did not permit a genetic interpretation of resistance. Van der Wal (1978) postulated the existence of minor genes, especially in *S. tuberosum* ssp. *andigena,* which would influence not only the segregation patterns but also the levels of resistance. Turner et al. (1983) reported variation of virulence within a pathotype of *G. pallida.* They also pointed out that the rate of increase will depend on the number of resistance genes present in the resistant hosts, in this case *S. vernei,* and the frequency of virulence in the nematode population.

But whatever the mechanism in the wild potato species evaluated in this study, resistance has been transferred to hybrid progenies. It is therefore clear that this nematode resistant germplasm is within the breeders' reach and can be utilised for potato improvement. The wild potato species of the central Andes of Peru and Bolivia are a valuable source of genetic diversity which must be conserved and evaluated, and ultimately used in potato breeding programmes.

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