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The Importance of the Bolivian Wild Potato Species in Breeding for *Globodera pallida* Resistance

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With one figure and 2 tables

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Abstract

Screening for resistance to the potato cyst nematode, *Globodera pallida*, in potatoes from Bolivia, was carried out in 1983 and 1984, using a mixture of four nematode populations representing pathotypes Pa_1, Pa_2 and Pa_3. From the 66 accessions of 17 species and subspecies evaluated, highly resistant genotypes were identified in 21 accessions from seven species. All had Pf/Pi values of 2 or less, whereas the susceptible control, *Solanum tuberosum* cv. 'Desiree', had Pf/Pi values of more than 20 in both tests. Two diploid wild species, *S. brevicaule* and *S. leptophyes*, showed the best resistant. The geographical distribution of resistant populations and the evolution of resistance in wild potato populations are discussed.

Key words: *Solanum* spec. — *Globodera pallida* — potato cyst nematode — potato breeding — genetic resources — wild species — resistance screening — evaluation studies — phytogeography

Resistance to the potato cyst nematode, *Globodera pallida* (Stone) Mulvey & Stone, is one of the principal objectives of potato breeding in the United Kingdom. Early work on resistance breeding concentrated on *G. rostochiensis* (Woll.), after resistance had been identified in *Solanum vernei* from north-west Argentina, and in *S. tuberosum* ssp. *andigena* (ELLENBY 1948, 1952). Even so, resistant European varieties were unknown before 1950 (VAN SOEST et al. 1983b). Since the recognition of two *Globodera* species in the early 1970s, there has been a concerted effort in Europe and South America to identify and use sources of resistance to *G. pallida*. These breeding efforts have paralleled germplasm collecting activities throughout the Andes of South America, but more particularly in Bolivia.

It is true that until the 1970s, the wild potatoes of Bolivia were less well known and understood biologically than those of other countries of South and Central America, even though some of the species that occur in Bolivia do have distributions which spread northwards into Peru, and southwards into Argentina. What is clear, however, is that the material collected in Bolivia has shown considerable promise as a source of cyst nematode resistance genes. Through evaluation studies of material collected in Bolivia in 1980 (VAN SOEST et al. 1983a), not only is there a much better understanding of the taxonomic and evolutionary relationships and distribution of the Bolivian wild species (HAWKES and HJERTING 1988) but genotypes resistant to *G. pallida* have been identified (VAN SOEST et al. 1983b, CHAVEZ 1984, DELLAERT and HOEKSTRA 1987, CHAVEZ et al. 1988).

There are 35 species and subspecies of wild potatoes in Bolivia (HAWKES and HJERTING 1988). Although the best sources of resistance to *G. pallida* have been found in species from Series Tuberosa, which are closest biologically to the cultivated potatoes, other species from Series Acaulia, Circaeifolia and Megistacroloba have also shown resistance. The apparent concentration of resistance genes to both *G. pallida* and *G. rostochiensis* in north-west Argentina has been commented upon by STONE (1979).

The spread of cyst nematode populations further north into Bolivia and Peru is reflected in the occurrence of nematode resistant potato species. Furthermore, reports of cyst nematode resistance seem to provide evidence in support of Vavilov's Law of Homologous Series (JACKSON 1988). Some of the best resistance has been reported by CHAVEZ et al. (1988) in *S. brevicaule* and *S. leptophyes*, with up to 98 % of individuals resistant to pathotypes P4A and P5A in *S. brevicaule*.

In this paper we report the results of resistance tests against pathotypes Pa_1, Pa_2 and Pa_3 of *G. pallida* in wild potato species from Bolivia. Furthermore, we have tried to relate the distribution of resistance genes to phytogeography, and to discuss the occurrence of resistance genes in wild potato populations from an evolutionary point of view.

Materials and Methods

Screening for resistance to *G. pallida* was carried out in 1983 and 1984 on potatoes from the University of Birmingham Potato Collection (coded PG), representing species collected in Bolivia in 1980 and 1981 by expeditions organized by scientists from Bolivia, West Germany, the Netherlands, the United Kingdom and Denmark (VAN SOEST et al. 1983a). Many accessions which showed apparent resistance in the preliminary evaluation of 1983 were included in the 1984 tests, in an attempt to confirm their resistance status. The 66 accessions represented 17 species and subspecies from five taxonomic series, and two natural interspecific hybrids (Table 1). All were wild species except for the one accession of *S. tuberosum* ssp. *andigena*. Seed from three of the accessions was produced from sib-matings at Birmingham whereas the remainder were from original seed collected in the wild.

Screening for resistance was carried out in both years on seedlings. Seeds were soaked overnight in gibberellic acid (1500 ppm), washed in water and sown in peat compost. One week after germination, seedlings were transplanted to individual 'Jiffy-7' peat pots, in which they continued growth for a further two weeks. They were then transplanted to 13 cm plastic pots containing a mixture of sterilized sand and loam soil (1 : 4 parts respectively).

A mixture of four *G. pallida* populations obtained from Rothamsted Experimental Station Nematology Department was used as inoculum. Three of the populations had been identified as pathotypes Pa_1 (Glarryford), Pa_2 (New Leake) and Pa_3 (Cadishead), but pathotype designation was not available for the population from G. M. Johnson's farm. Cysts had been stored for variable lengths of time at 5 °C. Viability was confirmed by hatching tests in water and counting juvenile nematodes. The populations were mixed in approximately equal proportions by cysts.

In the 1983 test, the number of eggs cyst^{-1} was estimated at 200, based on counts from five samples of a suspension of eggs attained by crushing a known number of cysts. In the 1984 test, four samples of 50 cysts each were taken at random and the number of eggs cyst^{-1} estimated; the average was 366 eggs cyst^{-1}.

The inoculation procedure was different in 1983 and 1984, although the seedlings were six weeks old at the time of inoculation in both tests. In 1983,

Table 1. Tuber-bearing *Solanum* species from Bolivia screened for resistance to *Globodera pallida*, pathotypes Pa_1, Pa_2 and Pa_3 in 1983 and 1984

Species	2n	Number of accessions screened
Series Circaeifolia		
S. circaeifolium ssp. *quimense*	24	1
Series Conicibaccata		
S. violaceimarmoratum	24	2
Series Acaulia		
S. acaule	48	5
Series Megistacroloba		
S. megistacrolobum	24	1
S. toralapanum	24	5
Series Tuberosa		
S. alandiae	24	5
S. berthaultii	24	11
S. brevicaule	24	6
S. leptophyes	24	5
S. microdontum		
ssp. *microdontum*	24	4
ssp. *gigantophyllum*	24	3
S. neocardenasii	24	2
S. okadae	24	1
S. oplocense	48	1
S. sparsipilum	24	8
S. sucrense	48	2
S. tuberosum ssp. *andigena*	48	2
Natural hybrids		
S. tarijense × *S. berthaultii*	24	1
S. megistacrolobum × *S. toralapanum*	24	1
Control		
S. tuberosum cv. 'Desiree'	48	

crushed cysts were used. The inoculum for each pot was prepared separately, consisting of 48 cysts which were soaked in water for 24 hours. A suspension of eggs, juveniles and crushed cysts was made up to 20 ml, and pipetted evenly in four equally spaced holes made around each seedling. Each hole was approximately 5 cm deep, and reached the root region. Crushed cysts were used so as to make it possible to differentiate between newly formed cysts and those from the inoculum at the final counting. In 1984, however, whole cysts were used as inoculum. Each seedling was inoculated with 40 full cysts, placed in four holes about 5 cm deep equally spaced around the seedling. The holes we refilled with dry sand.

In both tests plants were not watered for 24 hours before and after inoculation, but were watered daily thereafter. At 10 weeks and 12 weeks after inoculation in the 1983 and 1984 tests respectively, watering was stopped and plants allowed to wilt. The haulms were removed, and the pot contents allowed to dry further. A standard extraction and evaluation method was used in the assessment of cyst production. Cysts were extracted by flotation in water using the Fenwick can. Although this method can lead to losses of cysts during recovery from soil and

Table 2. Potato species from Bolivia resistant to *Globodera pallida*, pathotypes Pa_1, Pa_2 and Pa_3, based on the ratio (Pf/Pi) of new cysts to inoculum

Species	PG No.	Collectors' No.*	Mean Pf/Pi ratio 1983	1984
Series Acaulia				
S. acaule	2423	HHA 6617	—	1
Series Megistacroloba				
S. megistacrolobum	2565	SAL 127	1	<1
Series Tuberosa				
S. brevicaule	2320	HHA 6468	1	<1
	2425	HHA 6619	<1	—
	2428	HHA 6620	1	<1
	2430	HHA 6621	1	<1
	2471	HHA 6690	<1	<1
	2476	HHA 6701	1	<1
S. leptophyes	2483	HAM 006	1	1
	2485	HAM 008	<1	1
	2490	HAM 027	1	1
	2492	HAM 032	1	1
S. sparsipilum	2383	HHA 6553	<1	—
	2411	HHA 6597	1	—
	2436	HHA 6627	—	1
	2437**	HHA 6627	1	—
	2462	HHA 6670	1	2
	2466	HHA 6671	1	1
S. sucrense	2498	HAM 069	—	1
	2501	HAM 089	1	2
S. tuberosum ssp. *andigena*	2542	SOA 006	—	1
cv. 'Desiree' (control)			>20	>20

* 1980 expedition teams:
HHA = Hawkes, Hjerting and Avilés
SOA = van Soest, Okada and Alarcón
SAL = van Soest, Alarcón and Landeo
HAM = Hondelmann, Astley and Moreira
All seedlings grown from seeds collected from the wild, except that accession marked **, which was from sib-matings

organic matter, it is reliable, efficient and widely used.

In the 1983 test, resistance screening was based on three seedlings from each accession, whereas in the 1984 test, screening was carried out on five seedlings. The resistance of each seedling was determined on the basis of the ability of cyst nematodes to reproduce on potato plants, using the Pf/Pi ratio, where Pi is the initial nematode population (i.e. number of cysts added as inoculum) and Pf the final population (i.e. number of cysts recovered after senescence of the potato plant). Plants with a Pf/Pi ratio of less than 2 were regarded as resistant. Accurate counts were made up to three times the initial inoculum, but above this only estimates were made. The *S. tuberosum* cultivar 'Desiree' was used as a susceptible control, although in this case plants were grown from tubers.

Results

Assessment of resistance to cyst nematodes

Apparent broad spectrum resistance to *G. pallida* pathotypes Pa_1, Pa_2 and Pa_3 was identified in 21 accessions (Table 2), representing seven species from three taxonomic series. All had mean Pf/Pi ratios of 2 or less in one or both tests, and in fact only two accessions, *S. sucrense* HAM 089 and *S. sparsipilum* HHA 6670 had scores of 2, in the 1984 test. In contrast the *S. tuberosum* cultivar 'Desiree' had Pf/Pi values of more than 20, which clearly demonstrate its extreme susceptibility to this mixture of cyst nematode populations. In the light of this multiplication of cysts on a susceptible host plant, the resistance shown by the thirteen accessions tested in both years of *S. brevicaule, S. leptophyes, S. sparsipilum, S. sucrense* and *S. megistacrolobum* is even more impressive. Pf/Pi values were obtained for one test only for the remaining apparent resistant accessions belonging to *S. brevicaule, S. sparsipilum, S. tuberosum* ssp. *andigena* and *S. acaule.* Conflicting values were obtained for *S. neocardenasii, S. oplocense, S. acaule* and *S. circaeifolium* ssp. *quimense.* In the case of *S. neocardenasii* (HHA 6496), original seed was available only for the 1983 test, whereas seed from sib-matings had to be used in 1984. In the first test, the mean Pf/Pi value was 3, but in 1984 it was only 1. The same pattern was also shown by *S. acaule* HHA 6604 and *S. circaeifolium* ssp. *quimense* HHA 6532. However this trend was reversed in *S. oplocense* HAM 164 where the results for the 1984 test (mean Pf/Pi = 3) were higher than in 1983 (mean Pf/Pi = 1), and upon which this accession was selected for a second evaluation. All other species and accessions showed much higher multiplication of cysts, and although the Pf/Pi values never reached those on cv. 'Desiree', it was relatively easy nevertheless to discriminate these genotypes as susceptible to potato cyst nematodes.

The levels of resistance found in certain Bolivian wild potato species to *G. pallida* pathotypes Pa_1, Pa_2 and Pa_3 is impressive and extensive. Clearly the best resistance is found in *S. brevicaule* and *S. leptophyes,* and in all but one accession of *S. sparsipilum.* The low level of cyst nematode multiplication on genotypes of these species, relative to that which was typical of the susceptible control variety 'Desiree', indicates that the resistance of these species is worthy of further investigation. The importance of the *S. brevicaule* genotypes is strengthened by the results from other screening tests. The *S. brevicaule* accessions used in the present study against three *G. pallida* pathotypes were the same as those screened by CHAVEZ (1984) and reported by CHAVEZ et al. (1988) against pathotypes P4A and P5A. Although SCURRAH and FRANCO (1985) equated P4A and P5A with pathotypes Pa_2 and Pa_3 respectively, the nematode populations used by CHAVEZ were altogether different from those used here. Even so, CHAVEZ et al. (1988) reported a very high frequency of resistant genotypes in the *S. brevicaule* material, which indicates its very high breeding value. It is interesting also to mention those species such as *S. alandiae, S. berthaultii, S. microdontum, S. okadae, S. violaceimarmoratum* and *S. toralapanum* which gave low resistance values. The first three of these are from lower altitudes. Can we assume that *G. pallida* has not been present in such altitudes and that the species have not evolved protective mechanisms to combat it? Species such as *S. okadae, S. violaceimarmoratum* and *S. circaeifolium* ssp. *quimense* grow in the very high rainfall ceja forest region, and again, the nematodes may not have been present in this phytogeographical region. It is more difficult even to hazard a guess at the apparent lack of resistance in *S. toralapanum,* since this species is very frequent in the same region as *S. brevicaule,*

which is extremely promising in its *G. pallida* resistance. These are questions which cannot yet be answered.

Undoubtedly, the screening tests themselves can be open to criticism, since they were carried out on seedlings, but comparisons with cyst multiplication on cv. 'Desiree' were made on the basis of the latter grown from tubers. PHILLIPS (1984, 1985) has outlined some of the inherent dangers in assessing quantitative resistance to cyst nematodes, including the effect of initial population density on the reproduc-

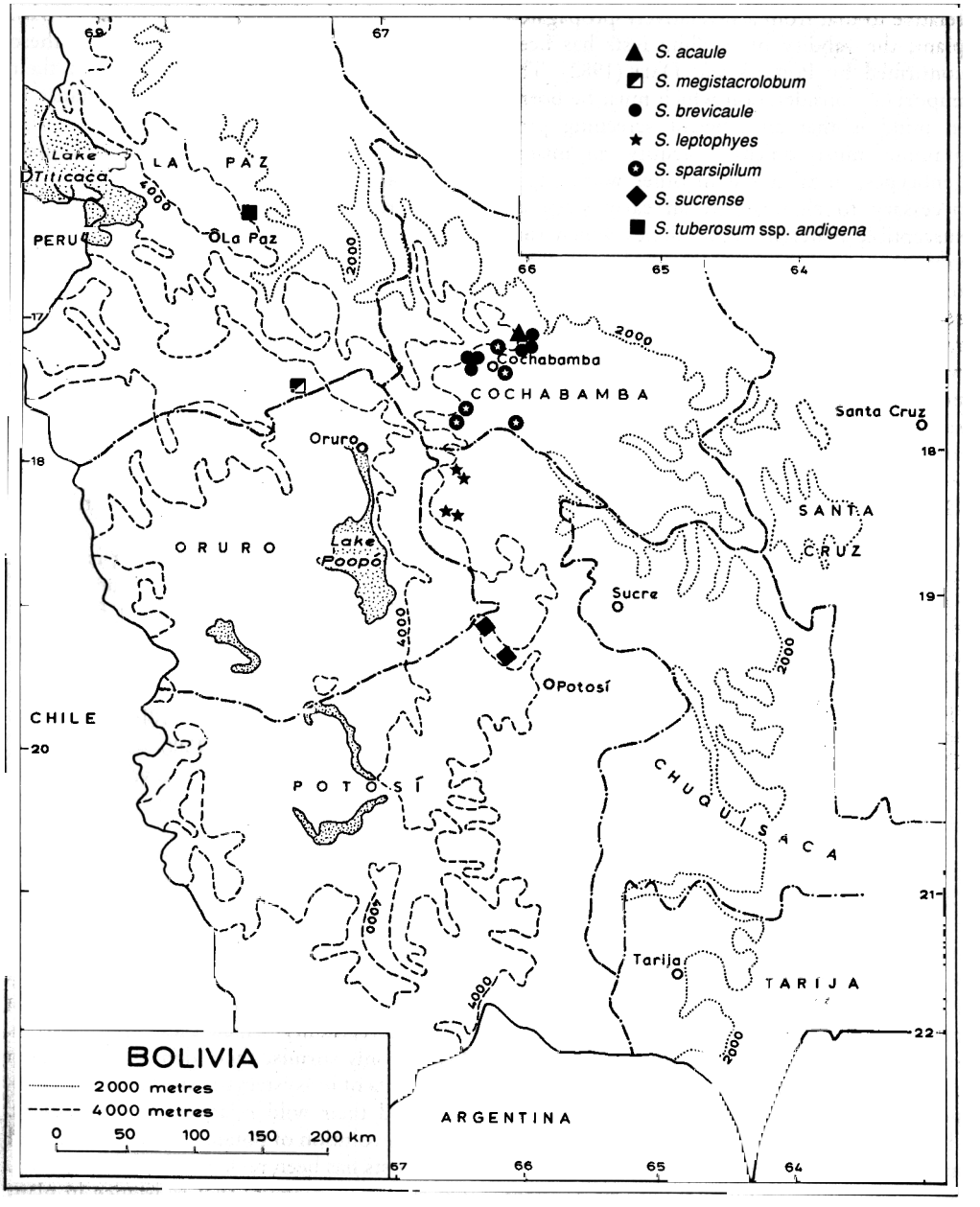

Fig. 1. The geographical distribution of 21 accessions from seven potato species resistant to *Globodera pallida* pathotypes Pa_1, Pa_2 and Pa_3 in Bolivia. Only five symbols are shown for *S. sparsipilum* as two accessions represent original seeds and seeds from sib-matings from the same collection

tion of *G. pallida*, and that in these experiments results can be variable because of genotype-environment interactions, due to the polygenic nature of resistance (SCURRAH and FRANCO 1985). Although some nematologists have criticized the use of seedlings in resistance testing, because of the restricted root system relative to that from a vegetatively-propagated plant, the validity of seedling tests has been confirmed by PHILLIPS and DALE (1982). The important consideration which must be borne in mind is that an efficient screening programme must quickly identify promising genotypes, or to put it in other words, it is necessary to eliminate at an early stage all susceptible materials. Any clones which survive a rigorous test can be evaluated again using tubers. It is therefore important to set selection criteria which allow the breeder rapidly to achieve this objective. Only in this way is it possible to screen germplasm for cyst nematode resistance, bearing in mind that resistance to this parasite is only one of many priorities in potato breeding.

Geographical distribution of resistant species

In order adequately to describe the geographical distribution of resistant species, it is necessary to comment upon the phytogeography of Bolivian wild species. They are found within a belt which runs north-south through central Bolivia (Fig. 1), with a concentration of species in the Departments of Chuquisaca (19 species and subspecies), La Paz (17) and Cochabamba (18), and fewer in Potosi (14), Santa Cruz (10), Tarija (9) and Oruro (5) (HAWKES and HJERTING 1988). No wild species have been found in the lowland tropical departments of Beni and Pando. The low number of species in Oruro can be explained by its high altitude, with most of the area of the department covered by high dry puna steppe, often with saline soils unsuitable for potatoes. HAWKES and HJERTING (1988) account for the potato richness of the other departments as a reflection of the range of altitude and ecological zones favourable for potatoes. In the present study, most of the accessions which showed resistance to *G. pallida* were collected in the area immediately to the north and south of Cochabamba, although other resistant materials were found in locations further to the north-west, and to the south and east (Fig. 1). Nevertheless, most of the accessions studied fall along a broad line north-west to south-east from La Paz to the region between Sucre and Santa Cruz. All the *S. brevicaule* and *S. leptophyes* materials came from the Cochabamba region, as did the majority of the *S. sparsipilum* accessions. These results at first sight seem to conflict with those of VAN SOEST et al. (1983b). However, closer inspection shows that these authors did not show *S. brevicaule* on their map, even though they noted Pa_3 resistance in their Table 2. They also screened a very large amount of material from Oruro and Potosi, southwards to the Argentine border. We had only three accessions (two of *S. sucrense* and one of *S. oplocense*) from that region. These three results fit well into the VAN SOEST et al. pattern as shown in their map. Again, our *S. sparsipilum* and *S. leptophyes* results accord with the VAN SOEST et al. resistance distribution for those species. On the whole then, our results agree well with the VAN SOEST et al. (1983b) work, but add an interesting new dimension in terms of the high incidence of *G. pallida* resistance in *S. brevicaule*, *S. leptophyes* and *S. sparsipilum*, especially in the La Paz and Cochabamba regions.

Another point worth mentioning is that all the *S. brevicaule* collections were found at very high altitudes (3650—3850 m) and from two general areas, both near Cochabamba. The *S. leptophyes* collections were from slightly lower altitudes (3200—3530 m) to the north of Potosi. The *S. sparsipilum* collections were from still lower altitudes (2380—3300 m), and were all from the Cochabamba valley region.

Discussion

The evolution of resistance to potato cyst nematodes in wild and cultivated plant populations is worthy of some consideration. Cultivated potatoes have originated from wild species, although it is not possible to say with complete certainty which these species were. We can only surmise their identity based upon the results of biosystematic studies of the cultigens and their wild relatives (HAWKES 1978). The co-evolution of potato cyst nematodes and their hosts has been reviewed by STONE (1985). Co-evolution suggests that resistance in plant hosts and virulence in nematodes is controlled by genes acting on a gene-for-gene basis. Such

interactions have been observed in relation to major resistance genes H_1 and H_2 (PARROTT 1982). However, such straightforward explanations cannot account for the variation in virulence which is encountered in *G. pallida* populations, and the polygenic nature of resistance to this nematode in potato species. One of the reasons why the pathotype concept of nematode populations, which describes races of a nematode species distinguished by inherited ability or inability to reproduce on specified lines of a host-plant species that embody different genes for resistance to the nematode (STONE 1985), is now being questioned because it is proving impossible to partition the variability of *G. pallida* populations within such a concept (STONE 1987). According to STONE (1985) the evolution of wild plant populations with resistance genes to nematode parasitism, and wild nematode populations with virulence genes and pathotypes, is a process which occurred in geological time. The outcome of this process is that we have available wild and cultivated potatoes which display resistance to potato cyst nematodes.

When we look at the distribution of *Globodera* populations throughout the Andes, it is apparent that most populations north of Lake Titicaca are *G. pallida*, whereas those to the south are mainly *G. rostochiensis* (EVANS et al. 1975). Why is it then, that wild species from Bolivia, considerably to the south of Lake Titicaca, such as *S. brevicaule* and *S. leptophyes*, show such good resistance to a wide range of *G. pallida* populations, which in the work reported by CHAVEZ et al. (1988), came from central and northern Peru, and in the work presented here, were British nematode populations? Furthermore, what are the actual selection pressures for resistance in nature? BRÜCHER (1961) reported finding cyst nematode on wild potatoes in Argentina. The validity of this report must, however, be questioned. In a detailed survey carried out in Peru and Bolivia in 1978, during the growing season, over 220 soil samples associated with cultivated and wild tuber-bearing *Solanum* species, as well as other solanaceous plants, were collected (EVANS, personal communication). Whereas cysts and females were found associated with cultivated potatoes, this was not so with wild species, except in one or two doubtful cases. In the light of such evidence, the existence of resistance genes in wild potato populations is very hard to explain, based on our present knowledge. If, as STONE (1987) has indicated, resistance to potato cyst nematodes evolved through co-evolution during geological time, the nature and distribution of the host-parasite interaction may well have been more extensive in the past than can be accounted for at the present time. Whatever may be the answer to this problem the evidence for resistance in wild potato species from Bolivia is of considerable importance from a breeding and genetic resources point of view. Resistance to *G. pallida* derived from *S. tuberosum* ssp. *andigena* and *S. vernei* may prove vulnerable to selection for virulence, and as a consequence, STONE (1985) argued for the breeding base for resistance to this parasite to be widened to include other sources. In this light the resistance identified in *S. brevicaule, S. leptophyes* and *S. sparsipilum* is important for potato breeding, as is that in *S. sucrense* because it is easier to cross with *S. tuberosum*. As CHAVEZ et al. (1988) have shown, such resistance can be transferred to hybrid progenies with *S. tuberosum*. The need for continued screening cannot be emphasized too strongly.

Zusammenfassung

Die Bedeutung bolivianischer Kartoffel-Wildarten für die Resistenzzüchtung gegen *Globodera pallida*

Es wurden in den Jahren 1983 und 1984 bei Kartoffeln aus Bolivien Prüfungen auf Resistenz gegen den cystenbildenden Nematoden *Globodera pallida* durchgeführt. Hierbei wurde eine Mischung aus 4 Nematoden-Populationen mit den Pathotypen Pa_1, Pa_2 und Pa_3 verwendet. Von 66 Herkünften aus 17 Arten und Unterarten erwiesen sich 21 Herkünfte aus 7 Arten als hochresistent. Im Gegensatz zur anfälligen Kontrollsorte 'Desiree' aus *Solanum tuberosum*, bei der Pf/Pi-Werte von über 20 zu verzeichnen waren, lagen die entsprechenden Werte der als hochresistent erkannten Herkünfte bei 2 und darunter. Die höchste Resistenz wurde bei den Arten *S. brevicaule* und *S. leptophyes* festgestellt. Die geographische Verbreitung der Resistenz und ihre Evolution in den Kartoffel-Wildarten werden diskutiert.

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