

# The importance of wild potato species resistant to the potato cyst nematode, *Globodera pallida*, pathotypes P<sub>4</sub>A and P<sub>5</sub>A, in potato breeding.

## II. The crossability of resistant species

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### Summary

Over 2400 pollinations were made to investigate the crossability relationships between cultivated potatoes, and wild diploid species from Series Tuberosa and Circaeifolia, as well as wild polyploid species in Series Tuberosa and Longipedicellata resistant to potato cyst nematode, *Globodera pallida* pathotypes P<sub>4</sub>A and P<sub>5</sub>A. Wild diploids in Series Tuberosa crossed easily with cultivated diploid species, except with *Solanum lignicaule* where most pollinations failed, and seed set was extremely low (0.2 seeds per pollination or less). It is suggested that this species is 1EBN. *S. capsicibaccatum* is clearly isolated from Series Tuberosa, but can form hybrids with *S. lignicaule*, which can act as a bridging species to *S. tuberosum* haploids. *S. gourlayi* and *S. oplocense* can be crossed with both subspecies of *S. tuberosum*, but *S. papita*, Series Longipedicellata is reproductively isolated from the tetraploid cultigens. The crossability data are discussed in the light of germplasm utilisation for breeding potato varieties resistant to potato cyst nematode.

### Introduction

The resistance to *Globodera pallida* pathotypes P<sub>4</sub>A and P<sub>5</sub>A of wild diploid potato species, interspecific hybrids between these wild species and diploid cultigens, *Solanum tuberosum* and *S. tuberosum* haploids, and hybrids involving other tetraploid and hexaploid species, has been reported earlier by Chavez et al. (1986). In this paper we report the crossability studies which were carried out to produce the hybrid progenies mentioned above.

Wide crosses in potato breeding between wild resistant species and varieties which are susceptible to a pest such as the cyst nematode, can be impor-

tant for potato improvement, provided that the chances of successful hybridisation and the frequency of F1 hybrids which are resistant and fertile are reasonably high. In the past, *S. vernei* has been used extensively for resistance to *G. rostochiensis* and some pathotypes of *G. pallida* (Ross, 1979; Uhrig & Wenzel, 1981). *S. vernei* and some of the other species identified by Chavez et al. (1988) are classified in Series Tuberosa, and are regarded as being more closely related to the cultivated species than wild species classified in other series. *S. capsicibaccatum*, a species from Bolivia and classified in Series Circaeifolia, has attracted notice because of its high resistance to *G. pallida*. In fact some genotypes have shown immunity to the most virulent

pathotype P<sub>5</sub>A. There are no reports to date, however, of crosses of this species with other species outside Series Circaeifolia. Chavez (1978) has reported that it was possible to obtain F1 hybrids in reciprocal crosses of *S. canasense*, *S. leptophyes* and *S. multidissectum* with *S. stenotomum*, suggesting a close phylogenetic relationship between them. As resistance to both pathotypes P<sub>4</sub>A and P<sub>5</sub>A of *G. pallida* has been identified in these species, their crossability relationships with cultivated diploids and haploids of *S. tuberosum* have been further studied. The haploids have been used extensively to transfer valuable characters from the diploids into the cultivated gene pool, and through 2n gametes, this can be achieved immediately in 4x × 2x crosses (Hougas & Peloquin, 1958; Mendiburu & Peloquin, 1977a, 1977b). The possibility for ploidy manipulation has been further enhanced by the identification of 2n gametes in wild species (Camadro & Peloquin, 1980; Quinn et al., 1974), through which wild species germplasm can often become more readily available for utilisation in potato breeding programmes.

## Materials and methods

Crosses were made between wild nematode resistant potato species (Chavez et al., 1988), and cultivated forms, and the species utilised are listed in Table 1. In general, single clone crosses were made, but some bulk pollinations were also made using *S. tuberosum* haploids. Nematode resistant and susceptible clones were crossed reciprocally, and self pollinations were also made on hexaploid *S. oplocense* and tetraploid *S. gourlayi* and *S. papita*. Intra- and interspecific reciprocal crosses within the same taxonomic series and between species in different series were attempted, at the same or different ploidy levels. Whenever possible, fresh pollen was used, although refrigerated pollen, stored at 5°C after drying, was used if no fresh pollen was available. All pollinations were made in an insect-proof glasshouse. In order to improve the success of pollinations, the cut-stem technique (McLean & Stevenson, 1952; Hanneman & Peloquin, 1967) was also used. Some pollinations were made on plants which had been grafted onto tomato stocks.

The crossability among the species used in this study was determined by the berry set, the number

Table 1. The *Solanum* species used in this study.

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

of plump seeds per pollination, the seed germination and the fertility of the F1 progenies, based on pollen stainability. Hybrid progenies were also screened for the occurrence of 2n gametes, based on the size of pollen grains (Quinn et al., 1974).

## Results

### *Wild diploids, Series Tuberosa*

Over 1400 pollinations were made between resistant wild species from Series Tuberosa and cultivated diploid species and *S. tuberosum* haploids (2x tbr) (Table 2). Crosses between cultivated diploids and *S. brevicaule*, *S. microdontum*, *S. sparsipilum* and *S. vernei* were more successful, in terms of seeds per pollination, when the wild species were the male parents. The converse was true for *S. leptophyes* and *S. multidissectum* in crosses with *S. stenotomum* and *S. phureja*, respectively. The most successful crosses were between *S. sparsipilum* and cultivated diploids, and produced an average of 51.6 seeds per pollination, which had a high germination rate. Seed production in reciprocal crosses of *S. canasense* and *S. stenotomum* was almost the same, with more than 30 seeds per pollination. There was more variation in response in crosses with *S. tuberosum* haploids, and seed set in these crosses was generally much lower overall. For example, in reciprocal crosses with *S. vernei*, there was almost equal success. The reciprocal crosses of *S. tuberosum* haploids and *S. leptophyes* produced as much seed as the cross *S. leptophyes* × *S. stenotomum*, whereas the reciprocal of this latter cross had a very low seed set of only 9.4 seeds per pollination.

Crosses between *S. lignicaule* and the diploid cultigens, represented by 179 pollinations, failed completely. Although 20 plump seeds were obtained from crosses in both directions with *S. phureja*, they failed to germinate. Attempts to hybridise *S. lignicaule* with *S. tuberosum* haploids were also unsuccessful. Although seven small seeds were harvested from 87 pollinations, they also failed to germinate. However an inter-clonal cross of *S. lignicaule*, used as a control, gave an average of over

21 seeds per pollination, thus demonstrating both the male and female fertility of this species, and that failure of the crosses with other species was not due to sterility.

### *Wild diploids, Series Circaeifolia and Series Tuberosa*

The reciprocal crosses between *S. capsicibaccatum* and *S. phureja*, *S. stenotomum* and *S. tuberosum* haploids were represented by 243 pollinations (Table 3). Only 13 seeds were formed in the cross *S. phureja* × *S. capsicibaccatum*, but these did not germinate. Parthenocarpic berries were formed however in the cross *S. tuberosum* haploids × *S. capsicibaccatum*. Control inter-clonal pollinations of *S. capsicibaccatum* produced an average of 21 seeds per pollination.

Since all attempts to hybridise *S. capsicibaccatum* and *S. lignicaule* with cultivated potatoes failed completely, a series of pollinations was made between these two species. From 120 reciprocal pollinations, a total of 209 plump seeds was obtained, even though the number of seeds per pollination was very low (Table 4). The cross was three times more successful, in terms of seeds per pollination when *S. capsicibaccatum* was the male parent. An important result was the successful hybridisation of the F1 hybrid *S. capsicibaccatum* × *S. lignicaule* with a high-yielding *S. tuberosum* FDR haploid clone, H.K.37, in which 2n pollen was produced, when this was used as male. However only 11 parthenocarpic berries were formed in other crosses between this hybrid and haploids, or when H.K.37 was the female parent.

### *Series Tuberosa (4x, 6x) and Series Longipedicellata*

Successful hybridisation between *S. gourlayi* and *S. tuberosum* was only achieved with the former species as the pollen parent. *S. gourlayi* was self-fertile, producing 40 seeds per pollination (Table 5).

Interploidy 6x × 4x crosses between *S. oplocense* and both subspecies of *S. tuberosum* were unsuccessful. The reciprocal 4x × 6x crosses result-

Table 2. Berry and seed production from reciprocal crosses between eight wild diploid species, Series Tuberosa, and *S. goniocalyx*, *S. phureja*, *S. stenotomum* and *S. tuberosum* haploids.

Reciprocal crosses	Pollinations	Berries	Seeds/Berry	Seeds/Pollination
<i>S. brevicaule</i>				
brc × gon	17	9	41.2	21.8
gon × brc	13	11	53.5	43.3
brc × phu	24	8	45.8	15.2
phu × brc	12	9	47.1	35.2
brc × stn	14	11	55.1	43.2
stn × brc	8	7	50.5	44.1
brc × 2x tbr	44	26	18.1	10.6
2x tbr × brc	41	26	13.2	8.4
<i>S. canasense</i>				
can × stn	11	10	39.1	35.5
stn × can	13	9	45.3	31.3
can × 2x tbr	16	11	19.8	13.6
2x tbr × can	10	8	21.8	17.5
<i>S. leptophyes</i>				
lph × stn	8	5	42.0	26.2
stn × lph	12	10	11.3	9.4
lph × 2x tbr	9	4	46.8	20.7
2x tbr × lph	34	26	25.8	19.7
<i>S. lignicaule</i>				
lgl × lgl	29	15	41.1	21.2
lgl × gon	11	0	0	0
gon × lgl	16	3	0	0
lgl × phu	34	5	0.8	0.1
phu × lgl	86	15	1.1	0.2
lgl × stn	13	0	0	0
stn × lgl	19	6	0	0
lgl × 2x tbr	20	0	0	0
2x tbr × lgl	67	18	6.3	0.1
<i>S. microdontum</i>				
mcd × gon	18	14	36.8	28.6
gon × mcd	15	15	41.3	41.3
mcd × phu	31	23	38.9	28.9
phu × mcd	10	8	40.6	32.5
mcd × 2x tbr	98	64	11.6	7.6
2x tbr × mcd	10	6	9.6	5.8
<i>S. multidissectum</i>				
mlt × phu	12	11	62.2	57.0
phu × mlt	10	6	54.8	32.9
mlt × 2x tbr	15	8	18.0	9.6
2x tbr × mlt	9	9	23.3	23.3
<i>S. sparsipilum</i>				
spl × gon	23	12	89.1	46.5
gon × spl	15	10	97.4	64.9
spl × phu	29	24	58.3	48.2
phu × spl	31	23	64.1	47.5
spl × stn	28	17	84.2	51.1
stn × spl	16	11	89.5	61.5
spl × 2x tbr	146	31	12.0	2.5
2x tbr × spl	139	92	20.6	13.5
<i>S. vernei</i>				
vrn × stn	15	8	73.6	39.2
stn × vrn	16	13	81.0	65.8
rn × 2x tbr	80	21	24.0	6.3
2x tbr × vrn	87	61	10.9	7.7

ed in 391 plump seeds from 43 pollinations, and the cross with ssp. *tuberosum* was slightly more successful than with ssp. *andigena*. However, the seeds from the cross with ssp. *tuberosum* were less viable. Self pollination of *S. oplocense* gave more than 40 seeds per pollination.

No success was obtained in the reciprocal  $4x \times 4x$  crosses of *S. papita* with both subspecies of *S. tuberosum*. However, interploid  $4x \times 2x$  crosses between *S. papita* and *S. tuberosum* haploids were successful, giving 387 plump seeds from 48 pollinations. Many of these seeds germinated, but all plants were sterile. The reciprocal cross produced only parthenocarpic berries. *S. papita* was self-fertile, with over 88 seeds per self pollination.

### Pollen stainability and 2n pollen

Pollen stainability and the occurrence of 2n pollen was determined for 293 plants from 14 F1 families

(Table 6). A total of 252 clones were identified with stainable pollen, and 41 clones were male sterile. Six clones were identified in which 2n pollen was produced.

Most of clones in the four families from crosses of *S. sparsipilum* with cultivated diploids and *S. tuberosum* haploids had stainable pollen, but some 12 clones (9.5%) were male sterile. Seven of these male sterile clones were derived from the crosses with the *S. tuberosum* haploids. Only one clone produced 2n pollen. The majority of *S. vernei* derived progenies had stainable pollen, and only four clones from crosses with the haploids were male sterile.

Considerable inter-clonal variation in the amount of stainable pollen was observed in progenies from *S. capsicibaccatum*  $\times$  *S. lignicaule*, although all were male fertile. Four clones were observed with 5%, 12%, 15% and 16% 2n pollen respectively. The trispecific hybrid of *S. capsicibaccatum*, *S. lignicaule* and a haploid of *S. tuberosum*

Table 3. The crossability of *S. capsicibaccatum*, Series Circaeifolia with *S. phureja*, *S. stenotomum* and *S. tuberosum* haploids in terms of berry and seed set.

Reciprocal crosses	Pollinations	Berries	Seeds/Berry	Seeds/Pollination
cap $\times$ cap	44	14	66.0	21.0
cap $\times$ phu	39	0	0	0
phu $\times$ cap	53	8	1.6	0.2
cap $\times$ stn	13	0	0	0
stn $\times$ cap	22	0	0	0
cap $\times$ 2x tbr	76	0	0	0
2x tbr $\times$ cap	40	23	0	0

Table 4. Berry and seed set from reciprocal crosses between *S. capsicibaccatum* and *S. lignicaule*, and hybrids between these two species and *S. tuberosum* haploids.

Reciprocal crosses	Pollinations	Berries	Seeds/Berry	Seeds/Pollination
cap $\times$ lgl	92	12	8.9	1.1
lgl $\times$ cap	28	7	14.5	3.6
(cap $\times$ lgl) $\times$ 2x tbr	20	2	0	0
2x tbr $\times$ (cap $\times$ lgl)	21	3	0	0
(cap $\times$ lgl) $\times$ 2x tbr (FDR)*	95	14	8.4	1.2
2x tbr (FDR) $\times$ (cap $\times$ lgl)	18	6	0	0

\* FDR: haploids of *S. tuberosum* producing 2n pollen by First Division Restitution, at a frequency of 5–20%.

Table 5. The crossability of *S. gourlayi* (4x) and *S. oplocense* (6x), Series Tuberosa, and *S. papita* (4x), Series Longipedicellata, with *S. tuberosum* ssp. *andigena* and ssp. *tuberosum* and *S. tuberosum* haploids in terms of berry and seed set in reciprocal crosses.

Reciprocal crosses and self pollinations	Pollinations	Berries	Seeds/Berry	Seeds/Pollination
<i>S. gourlayi</i>				
grl × tbr	24	0	0	0
tbr × grl	109	88	31.2	25.2
grl selfed	6	3	80.0	40.0
<i>S. oplocense</i>				
opl × adg	51	0	0	0
adg × opl	21	9	15.5	6.7
opl × tbr	23	0	0	0
tbr × opl	22	12	20.9	11.4
opl selfed	8	5	66.8	41.8
<i>S. papita</i>				
pta × adg	20	0	0	0
adg × pta	16	0	0	0
pta × tbr (4x)	15	0	0	0
tbr (4x) × pta	12	0	0	0
pta × 2x tbr	48	22	17.5	8.1
2x tbr × pta	27	10	0	0
pta selfed	60	45	117.7	88.3

Table 6. Pollen stainability, male sterility and 2n pollen in 293 clones from 14 F1 families derived from crosses between wild diploid, tetraploid and hexaploid potato species and diploid and tetraploid cultivated potatoes.

Crosses from which F1 families derived	No. clones studied	No. clones with stainable pollen	No. male sterile clones	No. clones with 2n pollen
<i>2x × 2x</i>				
spl × gon <sup>1</sup>	24	22	2	0
spl × phu <sup>1</sup>	42	41	1	0
spl × stn <sup>1</sup>	21	19	2	0
spl × 2x tbr <sup>1</sup>	39	32	7	1
vrn × stn <sup>1</sup>	10	10	0	0
vrn × 2x tbr <sup>1</sup>	23	19	4	0
cap × cap <sup>1</sup>	19	19	0	0
cap × lgl <sup>1</sup>	28	28	0	4
(cap × lgl) × 2x tbr FDR	12	5	7	1
<i>4x × 4x</i>				
adg × grl	29	29	0	0
4x tbr × grl	21	21	0	0
<i>4x × 6x</i>				
adg × opl	5	5	0	0
4x tbr × opl	2	2	0	0
4x × 2x				
pta × 2x tbr	18	0	18	0
Totals	293	252	41	6

<sup>1</sup> Includes reciprocal crosses.

produced seven male sterile clones (58%), but the fertile clones had low stainable pollen. One clone had 8%  $2n$  pollen.

Although no male sterility was found in hybrids between *S. oplocense* and the two subspecies of *S. tuberosum*, the frequency of stainable pollen ranged from only 5% to 9%. All hybrid clones derived from *S. gourlayi* were male fertile, whereas all those from *S. papita* were male sterile.

## Discussion

The results of interspecific hybridisation between the seven wild diploid species from Series Tuberosa, namely *S. brevicaula*, *S. canasense*, *S. leptophyes*, *S. microdontum*, *S. multidissectum*, *S. sparsipilum* and *S. vernei*, with cultivated diploid potatoes clearly demonstrate the close crossability relationship between them. It also appears that the wild diploid species involved in these crosses have a high degree of bilateral crossability with the diploid cultigens, but a lower degree with *S. tuberosum* haploids. This group of seven species certainly has great potential value from the practical breeding point of view, since the valuable resistance they have to *G. pallida* can be transferred to the cultivated gene pool (Chavez et al., 1988).

However, diploid *S. lignicaule* could not be hybridised with diploid cultivated species. This suggests that *S. lignicaule* has a different Endosperm Balance Number (EBN) from the cultivated diploids, which has already been established through the work of Johnston & Hanneman (1980) and Johnston et al. (1980). *S. lignicaule* appears to be 1EBN, as is *S. capsibaccatum* based on the crossability evidence, although the case for this latter species is much more tentative because it is much more isolated from Series Tuberosa. The successful hybridisation of *S. capsibaccatum* and *S. lignicaule*, which has never been reported before indicates that these two species may have a closer phylogenetic relationship than their assignment to different taxonomic series would suggest, as proposed by Hawkes (1978). However, when these species were compared in the glasshouse and in the field, they showed many characters in common.

Certainly the crossability data suggest that a revision of their taxonomic status is warranted, and furthermore, the results are also further evidence of the genomic differentiation between Series Tuberosa and Series Circaeifolia, as shown by crosses between *S. capsibaccatum* and cultivated diploids. It is interesting to note that *S. lignicaule* was an efficient bridging species in crosses of *S. capsibaccatum* and *S. tuberosum* haploids, thus effecting the transfer of nematode resistance (Chavez et al., 1988).

Hybrid progenies were obtained when *S. gourlayi*, *S. oplocense* and *S. papita* were crossed with cultivated potatoes, but a distinct unilateral incompatibility was manifested. The low fertility of the *S. oplocense* hybrids is different from that reported by Astley & Hawkes (1978), where fertile F1 hybrids were produced from reciprocal crosses of *S. oplocense* and *S. tuberosum* ssp. *andigena*. However, these workers used tetraploid cytotypes of *S. oplocense* from Bolivia, whereas hexaploid nematode resistant cytotypes from north west Argentina were the parental materials in this study, and would only cross with the tetraploids in one direction only. The low level of fertility of the *S. tuberosum* × *S. oplocense* hybrids can be attributed to their assumed pentaploid nature.

All F1 progeny from the cross of *S. papita* and *S. tuberosum* haploids were sterile. Although the ploidy level of the progeny was not determined, it can be assumed that they were triploid, as reported by Marks (1958) and Ramanna & Abdalla (1970) for progeny from crosses between tetraploid Longipedicellata species and Tuberosa diploids. The failure of *S. papita* to hybridise with tetraploid cultigens confirms the reports of Woodward & Jackson (1985). Based on this evidence, *S. papita* appears to be a 2EBN species, as is the case with  $4x \times 2x$  crosses of *S. acaule* with *S. tuberosum* haploids (Johnston & Hanneman, 1980) and crosses with cultivated diploids (Hermsen, 1966).

The use of haploids in potato breeding has been emphasised by Hermsen & Verdenius (1973), Mendiburu & Peloquin (1977a, 1977b) and by Ramanna (1979, 1983). The potential breeding of haploids for introducing alien germplasm into *S. tuberosum* directly at the diploid level has also been

pointed out by Den Nijs & Peloquin (1977) and Peloquin (1981). Even though crosses of the wild diploids with haploids were not as successful as crosses with diploid cultigens, nevertheless hybrid progenies resistant to *G. pallida* have been produced (Chavez et al., 1988).

The requirements of modern potato breeding programmes are such that it is increasingly necessary to resort to wide crosses to transfer genetic resistance to pests such as the potato cyst nematode. The results reported here, and the screening of the progeny from these hybridisations show that breeders will be able to utilise wild species relatively efficiently for potato improvement. The use of some species through conventional breeding techniques may be quite difficult but not totally impossible. Some of the biotechnological procedures outlined by Jackson (1986) will undoubtedly further unlock the vast store of genetic diversity which the wild species of potato represent, making them available to the plant breeder.

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