

The breeding potential of wild potato species resistant to the potato tuber moth, *Phthorimaea operculella* (Zeller)

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Summary

The potato tuber moth, *Phthorimaea operculella* (Zeller) is an important pest of potatoes in the field and in stores in warm environments throughout the world. In this study genetic resistance to potato tuber moth was identified in clones of *Solanum sparsipilum* (coded MBN) originally developed for resistance to bacterial wilt and root-knot nematode. Resistance to this pest in *S. sucrense* and *S. tarijense* as well as *S. sparsipilum* was exploited in wide crosses with diploid and tetraploid cultivated potatoes, and haploids derived from *S. tuberosum*; hybrid progenies were produced. Crosses between resistant *S. pinnatisectum* or *S. commersonii* and cultivated potatoes failed completely, although *S. commersonii* did hybridise with two bridging species *S. lignicaule* and *S. capsicibaccatum* which are slightly compatible with cultivated potatoes. Resistance to potato tuber moth was transferred to all progenies except those in which *S. tarijense* was the resistant parent. The development of potatoes resistant to potato tuber moth is discussed in the context of population breeding for the lowland tropics.

Introduction

The potato tuber moth (PTM), *Phthorimaea operculella* (Zeller), family Gelechiidae, is one of the most damaging potato pests in the world. In many tropical regions it is a major problem in potato stores for seed and ware or consumer potatoes (Couto et al., 1983; Haines, 1977), but severe infestations have also been reported in cooler areas such as in highland areas of Peru, Colombia, Nepal and Kenya. Potato tuber moth is now found in every developing country where potatoes are grown (International Potato Center, 1984). Experience with control measures has shown that it is unrealistic to rely solely on control with insecticides

as resistance to these compounds develops quickly in any tuber moth population. Furthermore, chemical control of this pest on ware potatoes carries considerable dangers for consumers, and overuse contaminates the environment.

The female moths lay eggs on developing tubers in the field, or on tubers in the store. Although tuber damage at harvest can be severe in some situations, where conditions have been favourable for the spread of the insect, or where farmers have allowed tubers to become uncovered as they develop, thus rendering such tubers unmarketable, the major problem with potato tuber moth lies in potato stores. Larval damage results in both weight and quality loss of the affected tubers, as wounds cause

shrinkage through increased transpiration, and also provide entrance for micro-organisms which in turn cause secondary infections (Raman & Palacios, 1982). In the field, culled tubers and volunteer plants provide an abundant food resource for *P. operculella* during non-cropping periods (Shelton & Wyman, 1980).

Research on alternative integrated control measures has been initiated (Raman & Palacios, 1983). This came as a response to the increased awareness of environmental problems caused by the excessive use of pesticides and as a recognition of the fact that no single control measure was able to overcome the problem of tuber moth infestations in fields and stores (Foot, 1976). Current measures of integrated pest management consist mainly of the combined use of insecticides, sex pheromone traps for attracting male moths, and insect species that parasitise *P. operculella* (Foot, 1976; Raman & Palacios, 1983; Sankaran & Girling, 1980).

No serious attempt has been made to utilise potato populations with genetic resistance to potato tuber moth, and in the germplasm of cultivated potatoes only some resistance of any consequence has been identified in *S. tuberosum* ssp. *andigena* (Raman & Palacios, 1982). Screening work involving wild potato species has been carried out at the International Potato Center (CIP), and has revealed the presence of a low frequency of moderately resistant genotypes. Out of 452 accessions tested, 27 showed significantly less larval damage than the controls, and pupation was only slight in comparison with other accessions. The reduced pupation was attributed to a factor of antibiosis effective in the tubers of the resistant accessions (Raman & Palacios, 1982). The observed resistance was not correlated however with total tuber glycoalkaloid content in the species accessions in question (Schmiediche, 1977; Osman et al., 1978; Raman & Palacios, 1982).

The identification of wild potato germplasm with resistance to potato tuber moth led to this study in which this resistance was transferred from wild to cultivated potatoes in a programme of wide crosses.

Materials and methods

The species used in this study are listed in Table 1. The Mexican diploid wild species *S. pinnatisectum* (Series Pinnatisecta) and the South American diploid wild species *S. commersonii* and *S. tarijense* (Series Commersonii), as well as the tetraploid wild species *S. sucrense* (Series Tuberosa) were used as sources of resistance to the potato tuber moth in the wide crossing programme. Additionally, 61 selected clones of the South American diploid weedy species *S. sparsipilum* (Series Tuberosa) with combined resistance to bacterial wilt (caused by *Pseudomonas solanacearum*) and root-knot nematode (*Meloidogyne incognita*) were screened for resistance to potato tuber moth. The clones with this combined resistance to bacterial wilt and root-knot nematode were coded MBN.

All the species listed above were utilised in a crossing programme to transfer resistance to potato tuber moth into cultivated potatoes. The cultivated crossing partners from Series Tuberosa were clones from the diploid species *S. goniocalyx*, *S. phureja* and *S. stenotomum*, haploids of *S. tuberosum*, and from tetraploid *S. tuberosum* ssp. *andigena*. Furthermore, the *S. sparsipilum* MBN clones were crossed with other MBN clones which had been derived from crosses between *S. sparsipilum*, *S. phureja* and the wild diploid *S. chacoense* (Series Commersoniana) in various combinations.

The programme of hybridisations

The genetic materials were maintained in an insect-proof glasshouse, and crosses between individual clones were carried out. Only when *tuberosum* haploids were used as male parents was pollen from about 10 clones bulked in order to overcome pollen fertility constraints. The cut stem technique (McLean & Stevenson, 1952) was used for the majority of crosses in order to promote a high frequency of berry set.

The parameters used to assess interspecific crossability were berry set, the number of plump seeds per berry, seed germination and the degree of F₁ fertility. Pollen stainability was used as a

measure of male fertility, following the method of Marks (1954), and 2n pollen production was assessed using the method of Quinn et al. (1974), in both hybrid progenies and parental genotypes.

Screening for resistance to potato tuber moth

(a) *Assessment of damage.* Female tuber moths lay their eggs on or near the 'eye' buds, and on hatching, larvae bore into the tubers via the 'eyes' and feed while boring tunnels or irregular galleries deep inside or just below the skin of the tubers. An accession was considered resistant when none of the tubers in any of the replications had more than one hole. Conversely, accessions were considered susceptible when just one of the tubers in any of the replications had more than one hole.

(b) *In an incubator.* Viable eggs of *P. operculella* were stored on filter paper inside a plastic petri dish, which was kept in a refrigerator at 5–6°C, until required for resistance testing. For each experiment, eggs were put in an incubator at 26°C for about two days after which hatching commenced. Four instar larvae were then transferred to whole tubers from each of the accessions to be evaluated. Six tubers as replicates were used from each acces-

sion. These tubers were kept in individual small plastic containers with tightly fitting lids, in order to prevent escape of larvae. The infested tubers were stored in an incubator at 24°C, and tuber damage as well as pupation were scored after 10 days. Tubers which did not show damage after 10 days were again scored three weeks later.

(c) *In a PTM-infested potato store.* Single tubers from each accession were placed in open paper bags which were put into wooden crates inside a PTM-infested potato store. Each crate contained 24 different clones plus a susceptible control. The experiment was replicated four times in a completely randomised design, each crate representing a single replication. The potato store was located in San Ramon, a mid-elevation site (800 m) in the tropical and humid environment on the eastern slopes of the Andes in central Peru, where CIP has one of its field stations. Temperatures ranged from 18–26°C during the course of the experiments. The potato tuber moth population was kept artificially high inside the store, by placing crates containing heavily infested tubers from a highly susceptible potato variety. An increase in the tuber moth population was fastest when the temperature ranged between 20 and 25°C. The life cycle of the insect was completed within three to four weeks (Haines,

Table 1. Tuber-bearing *Solanum* species used in wide crosses to transfer resistance to potato tuber moth, *P. operculella*, to hybrid progenies.

Species	Abbreviation	Series	Ploidy	Status
<i>S. capsicibaccatum</i>	cap	Circaeifolia	2x	wild
<i>S. chacoense</i>	chc	Commersoniana	2x	wild
<i>S. commersonii</i>	cmm	Commersoniana	2x	wild
<i>S. tarijense</i>	tar	Commersoniana	2x	wild
<i>S. pinnatisectum</i>	pnt	Pinnatisecta	2x	wild
<i>S. lignicaule</i>	lgl	Tuberosa	2x	wild
<i>S. sparsipilum</i>	spl	Tuberosa	2x	wild
<i>S. sucrense</i>	scr	Tuberosa	4x	wild
<i>S. goniocalyx</i>	gon	Tuberosa	2x	cultivated
<i>S. phureja</i>	phu	Tuberosa	2x	cultivated
<i>S. stenotomum</i>	stn	Tuberosa	2x	cultivated
<i>S. tuberosum</i>				
spp. <i>andigena</i>	adg	Tuberosa	4x	cultivated
ssp. <i>tuberosum</i>	tbr	Tuberosa	4x/2x	cultivated

1977; Raman, 1980). Tuber damage was evaluated three months after starting the experiment, and the susceptible controls were evaluated first in each crate.

Results

The results from the interspecific hybridisation studies and resistance testing are closely linked. The former provided progenies for resistance testing, and through the latter, resistant genotypes were identified for use in wide crosses. However, it is convenient to consider these two aspects separately, and cross reference is made where appropriate.

Interspecific hybridisation for the production of PTM resistant families

The six *S. sparsipilum* MBN clones resistant to potato tuber moth (Table 5) were successfully crossed with the other MBN clones of interspecific origin between *S. sparsipilum*, *S. chacoense* and *S. phureja* (Table 2). The 11 combinations resulted in 3375 viable plump seeds, although the number of pollinations was not recorded. The resulting families were labelled PTM.1 to PTM.11. The same six clones were further intercrossed reciprocally with *S. goniocalyx*, *S. phureja* and *S. stenotomum*, as

well as with *tuberosum* haploids. The hybrid families were labelled PTM.12 to PTM.33, and the data are given in Table 3. In general crosses between *S. sparsipilum* and diploid cultigens were successful, although the number of seeds per pollination did vary between the different crosses. The lowest seed set was in crosses with *S. phureja*. With the other two diploid cultigens, there were reciprocal differences in seed set, which was lower when *S. sparsipilum* was the female parent. Seed set was extremely low (0.2 seeds per pollination) when *tuberosum* haploids were the female parent, but much higher in the reciprocal, even though this was still lower than in the other crosses.

Crosses of *S. tarijense* with *S. phureja*, *S. stenotomum* and *tuberosum* haploids which represent hybridisation between different taxonomic series, yielded normal berries with viable seeds (PTM.40–45), although the cross with haploids failed when *S. tarijense* was the female parent. All attempts to hybridise *S. pinnatisectum* and *S. commersonii* with cultivated diploids and *tuberosum* haploids failed completely. *S. commersonii* was however hybridised as female with *S. capsicibaccatum* and *S. lignicaule* both of which were also resistant to potato cyst nematode (Chavez et al., 1987a). Hybrid families were labelled PTM.38 and 39 (Table 3).

S. sucrense, as pollen parent, was successfully crossed with *S. tuberosum* ssp. *andigena* (PTM.34–37), but it did not function as a female (Table 3). Self-pollinations of *S. sucrense* produced an aver-

Table 2. The seed production from crosses between *S. sparsipilum* MBN clones resistant to potato tuber moth, *P. operculella*, and interspecific hybrid MBN clones of *S. sparsipilum*, *S. chacoense*, *S. phureja* and *S. tuberosum*.

Cross	Pedigree	No. seeds obtained	Family code
spl × (spl × chc)	MBN 4.188 × MBN 5.2	270	PTM.1
spl × [(spl × phu) × tbr]	MBN 4.69 × MBN 11.44	180	PTM.2
spl × [(phu × spl) × spl]	MBN 4.41 × MBN 9.67	276	PTM.3
spl × [(spl × phu) × spl]	MBN 4.188 × MBN 8.29	360	PTM.4
spl × [(spl × phu) × spl]	MBN 4.41 × MBN 9.75	260	PTM.5
spl × (phu × spl)	MBN 4.69 × MBN 8.29	321	PTM.6
spl × [(spl × phu) × spl]	MBN 4.90 × MBN 9.75	410	PTM.7
spl × [(spl × phu) × spl]	MBN 4.41 × MBN 10.50	252	PTM.8
spl × (spl × chc)	MBN 4.188 × MBN 5.10	259	PTM.9
spl × [(spl × phu) × spl]	MBN 4.41 × MBN 10.25	267	PTM.10
spl × (phu × spl)	MBN 4.188 × MBN 9.63	520	PTM.11

age of 32 seeds per pollination, giving PTM families 46 and 47.

Pollen stainability and production of 2n pollen

Pollen stainability was determined for 2559 clones from 47 PTM families. A total of 2420 clones showed stainable pollen, whereas 139 clones were apparently male sterile (Table 4). Some 23 clones only (less than 1%) had 2n pollen. A high frequency of male sterility was found in the inter-series hybrids between *S. commersonii* and *S. capsibaccatum* or *S. lignicaule*. Furthermore, these hybrids did not set berries under field conditions.

Resistance of *S. sparsipilum* to potato tuber moth

Six of the 61 MBN clones of *S. sparsipilum* tested in the potato store in San Ramon were significantly less damaged than the control varieties, and were selected as resistant. Their mean tuber damage ranged from 0.25 to 1.0 holes per tuber (Table 5). This level of damage was approximately the same as shown by the resistant species *S. sucrense*, *S. commersonii* and *S. tarijense* in the same test. The remaining 55 *S. sparsipilum* clones showed variation in tuber damage, from 1.25 to 10 holes per tuber, whereas the susceptible control varieties DTO-33 and Desiree had a mean tuber damage of 7.50 and 7.75 holes per tuber respectively.

Table 3. Berry and seed production in wide crosses between diploid and tetraploid cultivated potatoes and wild species resistant to potato tuber moth, *P. operculella*.

Cross	No. pollinations	% Berry set	Seeds/berry	Seeds/ pollination	Family code (PTM)
gon × spl	27	89.0	47.0	41.7	16
spl × gon	25	76.0	29.0	22.0	17
phu × spl	121	65.5	17.5	11.4	14, 30
spl × phu	91	52.5	22.0	11.5	15, 29
stn × spl	161	77.6	46.8	36.4	12, 20, 25, 32
spl × stn	101	69.8	42.5	30.3	13, 21, 24, 31
2x-tbr × spl	209	77.5	0.3	0.2	18
spl × 2x-tbr	200	65.1	11.1	7.3	19, 22, 23, 26, 27, 28, 33
phu × tar	15	80.0	34.0	27.2	41
tar × phu	32	47.0	14.0	6.5	40
stn × tar	28	93.0	10.4	9.6	45
tar × stn	39	79.0	15.2	12.0	44
2x-tbr × tar	45	73.5	3.3	2.4	42, 43
tar × 2x-tbr	51	32.5	0	0	
phu × pnt	35	0	0	0	
pnt × phu	32	0	0	0	
stn × pnt	25	0	0	0	
pnt × stn	18	0	0	0	
phu × cmm	36	0	0	0	
cmm × phu	16	94.0	0		
2x-tbr × cmm	21	62.0	0	0	
cmm × 2x-tbr	74	68.0	0	0	
adg × scr	108	52.2	38.7	19.6	34, 35, 36, 37
scr × adg	58	34.0	0	0	
scr selfs	29	68.4	45.5	32.0	46, 47
cmm × cap	24	97.0	21.5	18.0	38
cap × cmm	92	0	0	0	
cmm × lgc	36	64.0	15.5	9.9	39
lgc × cmm	28	0	0	0	

The *S. sparsipilum* clones found to be resistant in San Ramon were tested in the incubator test (Table 5). Their resistance was confirmed, but damage in the incubator test was less than under conditions of natural infestation. The level of damage in *S. commersonii* and *S. tarijense* was higher than the *S. sparsipilum* clones in this test, but *S. sucrensis* again showed no damage whatsoever. Tuber damage was also considerably lower on the susceptible controls in the incubator test. The type of resistance was identified as feeding resistance or antibiosis.

Resistance of hybrid progenies of S. sparsipilum with MBN clones and cultivated diploids

A total of 501 clones from the families PTM.1 to PTM.11 was evaluated for resistance in both the incubator and potato store tests (Table 6). In the infested store, both DTO-33 and Desiree were completely destroyed by the larvae, but 171 clones (34%) resistant to *P. operculella* were selected. In the incubator test, 78% of the clones showed resist-

ance. These results indicate the importance of testing under conditions of natural infestation. Eleven of the clones which had shown resistance in the potato store test proved to be susceptible in the incubator test, and must be regarded as escapes in the former test. Consequently only 160 clones (32%) showed resistance in both tests. The proportion of resistant clones in the different families varied between 13 and 86%. Two of the highest levels were produced in progenies involving *S. sparsipilum* MBN 4.41 (PTM.3 and PTM.10), whereas MBN 4.69 gave the lowest proportion (PTM.2). The pedigrees of these PTM families are given in Table 2.

Fifteen hybrid families with a total of 1184 clones, resulting from crosses between *S. sparsipilum* and cultivated diploids or *tuberosum* haploids (PTM.12–15, 15C, 16–19, 22, 23, 26–28 and 33), were tested in the potato store, and 115 clones were identified as resistant (Table 7). Resistance ranged between 1% and 30% of clones between families. Four resistant clones (8.8%) were found in a chromosome-doubled hybrid family derived from a *S.*

Table 4. The occurrence of stainable pollen and 2n pollen in hybrid families (PTM) with resistance to the potato tuber moth, *P. operculella*.

PTM families	Cross	No. clones studied	% clones with stainable pollen	No. clones with 2n pollen
1, 9	spl × (spl × chc)	27	96	0
6, 11	spl × (phu × spl)	26	92	0
3	spl × [(phu × spl) × spl]	19	100	0
4, 5, 7, 8, 10	spl × [(spl × phu) × spl]	70	93	1
2	spl × [(spl × phu) × tbr]	3	100	0
12, 13, 20, 21	spl × stn*	722	98	7
24, 25, 31, 32				
14, 15, 29, 30	spl × phu*	306	88	
16, 17	spl × gon*	184	93	1
18, 19, 22, 23	spl × 2x-tbr*	341	97	3
26–28, 33				
40, 41	tar × phu*	151	99	0
42, 43	2x-tbr × tar	34	100	1
44, 45	tar × stn*	69	100	1
34–37	adg × scr	369	99	0
46, 47	scr selfs	78	99	1
38	cmm × cap	65	43	2
39	cmm × lgl	23	65	5

* Includes reciprocal pollinations.

sparsipilum × *S. phureja* cross (PTM.15C), which was only about one third that which had been found among the diploids of the same family (PTM.15). It is interesting to note that the highest proportion of resistant clones from these 15 families was found in those in which *S. sparsipilum* MBN 4.69 was the resistant parent, whereas in families PTM.1 to PTM.11, this clone gave progeny with a low frequency of resistant genotypes.

Resistance in interspecific hybrids

A total of 287 clones from families PTM.36, 38, 39, 42, 43 and 47) were screened in the potato store, but only 20 clones (7%) were resistant (Table 7). Thirteen of the clones were from a selfed *S. sucrense* family (PTM.47). Less than 2% resistant clones were recorded in hybrid families derived from crosses between *S. commersonii* and *S. capsicibaccatum* (PTM.38) or *S. lignicaule* (PTM.39).

Table 5. Mean tuber damage, expressed as holes per tuber, of six *S. sparsipilum* MBN clones and resistant and susceptible potatoes after exposure to the potato tuber moth, *P. operculella*, in an infested potato store and in an incubator test.

Clone	Mean tuber damage (holes per tuber)	
	Infested potato store	Incubator test
spl MBN 4.41	0.50 a	0.16 a
spl MBN 4.69	0.25 a	0.16 a
spl MBN 4.90	1.00 a	0 a
spl MBN 4.48	0.50 a	0.16 a
spl MBN 4.97	1.00 a	0.33 a
spl MBN 4.188	0.50 a	0.16 a
scr (resistant)	0 a	0 a
cmm (resistant)	0.50 a	0.50 a
tar (resistant)	0.50 a	0.66 a
tbr DTO.33 (susceptible)	7.50 b	2.33 b
tbr cv. Desiree (susceptible)	7.75 b	2.50 b

Values are the means of four replicates in the infested storage test, and means of six replicates in the incubator test. Means in the same column followed by the same letter are not significantly different at the 5% level, according to Duncan's Multiple Range Test.

There was no resistance in two of the families derived from crosses between *tuberosum* haploids and *S. trajense* (PTM.42 and 43). Only five clones out of 98 from family PTM.36 (*S. tuberosum* ssp. *andigena* × *S. sucrense*) showed no tuber damage.

Agronomic value of hybrids

Long stolons were commonly observed in hybrids between wild species and cultivated diploids, but in the majority of hybrids that had a *tuberosum* haploid as one of the parents, the stolons were short. Hybrids with a cultivated tetraploid or haploid parent showed, in general, good performance in terms of plant vigour, tuber yield and tuber uniformity. Hybrid vigour and uniformity of aerial parts were observed in the diploid families derived from crosses between wild species and *tuberosum* haploids. Plants displayed broad *tuberosum*-like leaves, and semi-erect growth habit also characteristics of *S. tuberosum* ssp. *tuberosum*. Early senescence and tuberisation were observed in hybrids from crosses of *S. sparsipilum* and *tuberosum* haploids. However, medium to late tuberisation as well as high

Table 6. The occurrence of resistance to the potato tuber moth, *P. operculella*, in 11 hybrid families derived from crosses between *S. sparsipilum*, *S. chacoense*, *S. phureja* and diploid *S. tuberosum*, after exposure in an infested tuber store and in an incubator test.

PTM family	No. clones evaluated	No. clones resistant		
		Store	Incubator	Both tests
PTM.1	40	17	31	14
PTM.2	24	5	14	3
PTM.3	42	23	35	21
PTM.4	37	17	23	16
PTM.5	49	11	39	10
PTM.6	50	8	41	8
PTM.7	74	15	63	15
PTM.8	31	7	22	7
PTM.9	24	13	18	13
PTM.10	36	31	36	31
PTM.11	94	24	69	22
Totals	501	171	391	160

berry set were recorded in hybrids of *S. sparsipilum* with *S. goniocalyx*, *S. phureja* or *S. stenotomum*, and among clones derived from crosses of *S. tuberosum* ssp. *andigena* and *S. sucrense*.

Flowering was extremely sparse in diploid hybrids that had a *tuberosum* haploid as a parent. In contrast, flowering was profuse in tetraploid hybrids derived from *S. tuberosum* ssp. *andigena* and *S. sucrense*. Likewise flowering was abundant in diploid hybrids which had resulted from crosses between resistant diploid clones and cultivated diploids.

Discussion

This work has demonstrated the feasibility of transferring genes for resistance to the potato tuber moth, *P. operculella*, from wild species to cultivated potatoes through interspecific hybridisation.

The wild species *S. sparsipilum* and *S. sucrense* could be hybridised directly with clones from the diploid and tetraploid cultivated species, to produce fertile and tuber moth resistant F₁ hybrids. However, resistance genes in *S. pinnatisectum* and *S. commersonii* were not introduced into the cultivated genepool due to the cross incompatibility of these species. Although it was possible to produce F₁ hybrids between *S. tarijense* and cultivated potatoes, all progenies were susceptible to potato tuber moth.

The success of the crosses involving *S. sparsipilum* and *S. sucrense* and cultivated potatoes can be explained by their close genomic relationship (Hawkes, 1978). *S. sparsipilum* has been regarded as one of the putative ancestors of tetraploid *S. tuberosum* ssp. *andigena* (Cribb & Hawkes, 1986). *S. sucrense* originated by natural hybridisation between the wild species *S. oplocense* and *S. tuberosum* ssp. *andigena* (Astley & Hawkes, 1979).

Table 7. The resistance of hybrid families derived from crosses between wild and cultivated potato species to the potato tuber moth, *P. operculella*, after exposure in an infested potato store.

PTM family	Cross	Resistant parent	No. clones evaluated	No. clones		% resistant
				Resistant	Susceptible	
PTM.12	stn × spl	spl MBN 4.69	100	13	87	13.0
PTM.13	spl × stn	spl MBN 4.69	75	11	64	14.6
PTM.14	phu × spl	spl MBN 4.69	72	7	65	9.7
PTM.15	spl × phu	spl MBN 4.69	54	16	38	29.6
PTM.15C*	spl × phu	spl MBN 4.69	45	4	41	8.8
PTM.16	gon × spl	spl MBN 4.69	99	6	93	6.0
PTM.17	spl × gon	spl MBN 4.69	83	12	71	14.6
PTM.18	2x-tbr × spl	spl MBN 4.69	15	3	12	20.0
PTM.19	spl × 2x-tbr	spl MBN 4.69	96	21	75	21.8
PTM.22	spl × 2x-tbr	spl MBN 4.188	100	1	99	1.0
PTM.23	spl × 2x-tbr	spl MBN 4.188	100	4	96	4.0
PTM.26	spl × 2x-tbr	spl MBN 4.41	89	9	80	10.1
PTM.27	spl × 2x-tbr	spl MBN 4.41	70	2	68	2.8
PTM.28	spl × 2x-tbr	spl MBN 4.188	86	5	81	5.8
PTM.33	spl × 2x-tbr	spl MBN 4.90	100		99	1.0
PTM.36	adg × scr	scr HHC 4596.3	98	5	93	5.1
PTM.38	cmm × cap	cmm OKA 507/4	64	1	63	1.5
PTM.39	cmm × lgl	cmm OKA 507/4	56	1	55	1.7
PTM.42	2x-tbr × tar	tar OKA 5886.2	24	0	24	0
PTM.43	2x-tbr × tar	tar OKA 5886.2	13	0	13	0
PTM.47	scr self	scr HHC 4596.1	32	13	19	40.6

* Hybrid clones from PTM.15 were treated with colchicine for chromosome doubling.

Crosses between *S. sucrense* and cultivated tetraploids produced vigorous and fully fertile F₁ hybrids, but only when the wild species was the pollen parent. Although genes for resistance to potato tuber moth are easily expressed in hybrids with tetraploid potatoes, as demonstrated in this work, the F₁ progenies do have some negative characteristics such as late maturity, long stolons and considerable inter-clonal variation with regard to tuber shape. The use of *tuberosum* haploids is worth considering in this context, since they would be expected to have fewer undesirable agronomic characteristics. Chavez (1984) has reported the successful hybridisation of F₁ hybrids resistant to potato tuber moth and *tuberosum* haploids, producing over 5000 seeds. This material has not been screened however for tuber moth resistance.

Despite being taxonomically distinct from the cultivated potatoes, *S. tarijense* shows some genetic affinities with these through successful crosses with *tuberosum* haploids and *S. phureja*, setting viable seeds and giving fertile F₁ hybrids. The differentiation between *S. tarijense* and cultivated potatoes would seem therefore to be due only to cryptic genic structural differences. The fact that resistance to potato tuber moth was not manifested in hybrid progenies of *S. tarijense* is difficult to explain, but could be due some aspects of the inheritance of resistance to this pest. Furthermore, chromosome studies were not made of the hybrid plants, so there is no indication of meiotic abnormalities.

The breeding potential of *S. commersonii* was disappointing since all attempts to hybridise this species with cultivated diploids and *tuberosum* haploids failed completely indicating strong bilateral incompatibility barriers between them. Nevertheless hybridisations between species from different taxonomic series was possible with the help of two bridging species, namely *S. lignicaule* and *S. capsicibaccatum* which both crossed with *S. commersonii*, and which have been shown to be slightly compatible with cultivated potatoes (Chavez et al., 1987b). However, these crosses with *S. capsicibaccatum* and *S. lignicaule* were possible only in one direction, indicating the presence of unilateral cross incompatibility, and many hybrid genotypes

were sterile. Further investigation of this incompatibility is merited, with a view to overcoming fertility problems in the progeny.

The high pollen stainability of many of the progenies is encouraging, and should lead to their efficient utilisation in breeding. Resistance to the potato tuber moth can be used easily at the diploid level, but must eventually be transferred into the tetraploid genepool. The low level of 2n pollen encountered in the progenies developed in this study is somewhat surprising, since studies at the University of Wisconsin by Quinn et al. (1974) and others have shown that the phenomenon of 2n pollen is widespread in the tuber-bearing solanums.

The identification of progenies resistant to potato tuber moth is important for the development of potatoes adapted to warm environments where *P. operculella* is a major problem. Progenies resistant to *P. operculella* are now available for inclusion in the populations for the lowland tropics through the population breeding strategy which is used at the International Potato Center (Mendoza, 1980a, 1980b; International Potato Center, 1984). The transfer of tuber moth resistance into hybrid progenies with cultivated potatoes is an important step towards the production of potato clones with combined resistance to potato tuber moth, bacterial wilt and root-knot nematode, adapted to such environments.

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