

Utilization of Tuber-bearing *Solanum* triploids in Studies of Species Differentiation

Lee, Heiyoung Kim and H. T. Erickson*
(Dongguk University, Seoul, *Purdue University, U.S.A.)

三倍體 塊莖形成 *Solanum*을 이용한 種의 區分에 관한 研究

金 惠 英 · H. T. Erickson*
(東國大 農生物學科 · *Purdue大)

ABSTRACT

Triploids of inter-and intra-specific hybrid of tuber-bearing *Solanum*, involving $4x$ *S. tuberosum*, *S. stoloniferum*, *S. fendleri* and *S. chacoense* and other diploid species were used to study the affinity between the species.

The number of multivalent formations in triploids depended on the cross combination. However, multivalent formation from triploids produced by $4x \times 2x$ crosses within *S. chacoense* did not differ from triploids from *S. tuberosum* ($4x$) \times *S. chacoense* ($2x$). Many of the triploid hybrids had 13 or more bivalents plus trivalents and quadrivalents indicating slight autosyndesis. As the basic chromosome number in potato is assumed to be 12, the slight excess pairing might be due to structural differences of chromosomes and eventually to non- or partial-homologous pairing.

Male fertility of triploid hybrids was very low (less than 7.2% stainable pollen) with exceptions of triploids, involving *S. tuberosum* \times *S. chacoense* (49.16%) and *S. chacoense* ($4x$) \times *S. chacoense* ($2x$) (30.25%). Pollen fertility was associated with chromosome affinity at first metaphase rather than with chromosome distribution at second metaphase. The large number of multivalents and high pollen fertility in the triploid hybrid of *S. tuberosum* \times *S. chacoense*, indicates a very high affinity of these two species.

INTRODUCTION

Controversy exists with reference to validity of species among tuber-bearing taxa in the genus *Solanum*. Existence of both sexual and vegetative reproduction in the genus probably contributes to this situation (Correll, 1962).

Structural differentiation between chromosome complements can provide information on degree of relationship as can be investigated in two ways; direct morphological comparison of the chromo-

somes, and the type and extent of pairing in hybrids involving different genomes. However, such studies are difficult in *Solanum* section *Tuberarium* for the following reasons. First, the chromosomes are small and chiasmata appear to be restricted to the ends of the short chromosomes (Magoon and Ramanujam, 1960), and in some case the chiasmata genetically controlled (Wang, 1971). Secondly, species chromosomes may differ only in cryptic structural differences. Accordingly, any set of 12 chromosome is usually capable of pairing

with any other set in species hybrids (Swaminathan, 1954). Furthermore, while polyploid species regularly form only bivalents at MI, their derived haploids show autosyndetic pairing in the majority of chromosomes (Marks, 1955).

Derived triploids of hexaploid *S. demissum* pair at meiosis in a way which suggest the presence of two genomes (Swaminathan and Howard, 1953). Similarly, chromosomes of interspecific triploids such as *S. stoloniferum* × *S. verrucosum* apparently segregate into two distinct genomes, one pairing and the other remaining as univalents. These three species are native to Mexico, indica-

ting that functional isolating mechanisms have existed in this restricted geographic area. Howard (1960) stated that there appears to be "more differentiation between the genomes of diploid species than was previously thought to be so." He encouraged further study including evidence from diploid × tetraploid crosses.

Some of the information in the literature on chromosome pairing at MI, and pollen fertility of diploids, triploids and tetraploids is shown in Table 1. Meiosis in diploid species and their hybrids is generally regular, twelve bivalents being found in most pollen mother cells. However meio-

Table 1. Meiotic chromosome associations and pollen fertility as reported in various species and hybrids

Species and Hybrids	Mean frequency per cell at MI				Pollen fertility (%)	References
	IV	III	II	I		
Diploid						
<i>S. tuberosum</i>	0	0.04	10.44	3.02	0.09	Matsubayashi 1960
<i>S. chacoense</i>	—	—	—	—	95	Swaminathan 1951
<i>S. chacoense</i>	0	0	12	0	—	Gilles 1955
Triploid						
<i>S. cardiophyllum</i>	0	8.15	4.35	2.92	41.97	Sanudo 1962
<i>X. × Vallis-mexici</i>	0	0.68	11.54	10.94	—	Marks 1954
<i>S. chaucha</i>	0	7.9	4.1	4.1	21	Lamm 1945
<i>S. commersonii</i>	0	5.76	7.88	4.16	—	Magoon and Ramanujam 1960
<i>S. acaule</i> × <i>S. chacoense</i>	0	4.10	8.72	6.40	sterile	Propack 1937
<i>S. acaule</i> × <i>S. tuberosum</i> (2x)	0	3.25	8.81	8.58	—	Hermesen and Ramanna 1969
<i>S. acaule</i> × <i>S. bulbocastanum</i>	0	0.44	12.40	10.46	—	Hermesen and Ramanna 1969
<i>S. tuberosum</i> × <i>S. chacoense</i>	0	2.46	9.00	7.60	17	Prakken and Swaminthan 1952
<i>S. verrucosum</i> × <i>S. stoloniferum</i>	0	1.46	10.54	9.56	—	Marks 1958
<i>S. fendleri</i> × <i>S. chacoense</i>	—	—	—	—	0	Clark 1929
<i>S. longipedicellatum</i> × <i>S. chacoense</i>	0	0.75	11.75	10.27	0.05	Kawakami et al. 1956
<i>S. longipedicellatum</i> × <i>S. schickii</i>	0	1.05	11.05	10.73	0	Matsubayashi 1955
Tetraploid						
<i>S. andigenum</i>	1.35	0.75	19.55	1.25	91	Lamm 1945
<i>S. tuberosum</i>	2.05	1.20	13.30	1.60	64.7	Lamm 1945
<i>S. tuberosum</i>	2.22	0.72	17.75	1.41	34.30	Swaminathan 1954
<i>S. longipedicellatum</i>	0	0	23.84	0.31	84.40	Matsubayashi 1955
<i>S. tuberosum</i> × <i>S. chacoense</i>	1.15	0	21.46	0.56	78	Prakken et al. 1952
<i>S. phureja</i> × <i>S. tuberosum</i>	1.40	0	20.64	1.12	65	Prakken et al. 1952

tic irregularities such as the presence of univalents, trivalents, quadrivalents, chromatin bridges, fragments, laggards and other abnormalities occur in a small percentage of microsporocytes (Lamm, 1945; Matsubayashi, 1960; Magoon et al., 1958; Marks, 1968; and Krishnappa, 1968).

Triploid hybrids should be useful in clarifying relationships between parent species through the number of trivalents formed during meiosis, and by their fertility.

MATERIALS AND METHODS

Tetraploids and diploids of several species were obtained from the U.S. Plant Introduction Station

at Sturgeon Bay, Wisconsin and crossed, using the tetraploids as pistillate parents. Triploids and their parents are listed in Table 2. Metaphase I was studied in 35 cells of each clone except in 73-5 (14 cells), and P.I. 189217 C. 19 (13 cells). Meiotic preparations were made using Matsubayashi's (1963) modified aceto-carmine technique, or the aceto-carmine smear method, following fixation in Farmer's fluid. Slides were made permanent by a freezing method (Johnson and Janick, 1962). Pollen fertility counts followed Mark's (1954) modified aceto-carmine glycerol jelly method. Pollen was germinated in a solution of 20% sucrose, 50 ppm H_2BO_3 and 200ppm $Ca(NO_3)_2$ using hanging drop technique (Mortenson et al., 1964).

Table 2. Triploid hybrids clones and their parentage

Triploid clones	Parentage (4x×2x)
50-3, 7	<i>S. stoloniferum</i> P.I. 161172× <i>S. tuberosum</i> haploid US-W 8093, 36
65-8, 9	<i>S. fendleri</i> P.I. 275158× <i>S. tuberosum</i> haploid (DH') US-W 5278
65-9, 1	65-9(<i>S.fendleri</i> P.I. 275158×US-W 5278)× <i>S. chacoense</i>
73-5, 9, 11	<i>S. stoloniferum</i> P.I. 161172× <i>S. chacoense</i>
103-1	<i>S. tuberosum</i> cv. Redskin× <i>S. chacoense</i>
7-1, 2, 3, 5, 6, 7	<i>S. chacoense</i> P.I. 189217 c. 18× <i>S. chacoense</i> P.I. 123124
8-1, 2, 3	<i>S. chacoense</i> P.I. 189217 c. 18× <i>S. chacoense</i> P.I. 197760
9-2	<i>S. chacoense</i> P.I. 189217 c. 19× <i>S. chacoense</i> P.I. 197760

DH': cross, *S. phureja* female×*S. tuberosum* haploid male

RESULTS AND DISCUSSION

Chromosome pairing: In triploids of *S. chacoense*, quadrivalents (0-1) appeared in some cells in addition to univalents (0-8), bivalents (0-11) and trivalents (4-12). The mean number of each is shown in Table 3. Analysis of variance of the number of multivalents (quadrivalents and trivalent) showed some clonal differences in triploid *S. chacoense* (Table 4 and Figure 1 and 2). Fewer multivalents in two clones, 7-2 and 7-7, would account for this difference.

Diploid *S. chacoense* had mostly bivalents (Figure 3). The tetraploid, had all classes well represented in most cells (Table 3 and Figure 4). Among

the progenies of tetraploid×diploid *S. chacoense*, clone 7-1 had 36 chromosomes plus 2 fragments.

The number of multivalents in triploids of interspecific crosses differed significantly at the 1% level (Table 5). However, triploids of *S. chacoense* did not differ from the interspecific triploid *S. tuberosum*×*S. chacoense* (Table 6). These two crosses produced the most multivalents, 8.25 and 8.49 respectively, a frequency equal to that found in natural triploids. For instance, Lamm (1945) observed 7.9 trivalents in naturally occurring triploid *S. chaucha* and Sanudo Palazuelos (1962) observed 8.08 and 8.23 trivalents in naturally occurring triploid *S. cardiophyllum*.

Multivalent frequency in triploid hybrids is used as evidence of relationship between two species

Table 3. Chromosome pairing at M₁ in triploid hybrids, and in diploid, triploid and tetraploid clones of *S. chacoense*

Clone	IV		III		II		I	
	No. ¹	SE ²	No.	SE	No.	SE	No.	SE
<i>S. stoloniferum</i> × <i>S. tuberosum</i>								
50-3	0		4.23(0.32)		7.77(0.32)		7.77(0.32)	
50-7	0		4.34(0.27)		7.66(0.27)		7.66(0.27)	
<i>S. stoloniferum</i> × <i>S. chacoense</i>								
73-5	0		2.57(0.36)		9.50(0.36)		9.29(0.40)	
73-9	0		3.74(0.26)		8.20(0.27)		8.37(0.28)	
73-11	0		3.89(0.28)		8.14(0.18)		8.06(0.31)	
<i>S. fendleri</i> × DH ³								
65-8	0		5.51(0.25)		6.74(0.26)		5.79(0.28)	
65-9	0		4.54(0.26)		7.71(0.31)		6.94(0.27)	
<i>(S. fendleri</i> × DH) × <i>S. chacoense</i>								
65-9-1	0		4.86(0.32)		7.60(0.38)		6.20(0.45)	
<i>S. tuberosum</i> × <i>S. chacoense</i>								
103-1	0		8.49(0.31)		3.60(0.33)		3.34(0.29)	
<i>S. chacoense</i> (3x)								
7-1 ⁴	0.43(0.09)		7.94(0.24)		4.40(0.35)		3.66(0.28)	
7-2	0.03(0.03)		7.60(0.30)		4.66(0.37)		3.77(0.25)	
7-3	0		8.60(0.21)		3.43(0.23)		3.34(0.22)	
7-5	0		8.83(0.23)		3.66(0.22)		3.74(0.28)	
7-6	0.06(0.04)		8.69(0.24)		3.43(0.26)		2.86(0.19)	
7-7	0.03(0.03)		7.66(0.28)		4.49(0.30)		3.94(0.28)	
8-1	0		8.51(0.23)		3.51(0.24)		3.43(0.23)	
8-2	0.02(0.03)		8.31(0.22)		3.77(0.24)		3.40(0.23)	
8-3 ⁵	0.06(0.04)		8.00(0.27)		4.06(0.29)		3.66(0.31)	
9-2	0.03(0.03)		8.37(0.22)		3.67(0.24)		3.46(0.22)	
<i>S. chacoense</i> (4x)								
189217 c. 18	3.26(0.23)		2.88(0.23)		11.53(0.55)		3.24(0.28)	
189217 c. 19	2.00(0.25)		5.00(0.32)		9.69(0.49)		5.61(0.50)	
<i>S. chacoense</i> (2x)								
133124	0		0.03(0.03)		11.89(0.07)		0.11(0.08)	

1) No.=mean number

2) SE=standard error

3) DH=cross, *S. phureja* × *S. tuberosum* haploid

4) 7-1=hyper-triploid (2n=36 + 2 fragments)

5) 8-3=abnormal overall morphology

(Hermsen and Ramanna, 1969). A maximum number of 12 trivalents was observed in several cells of the triploid *S. chacoense* as well as triploid *S. tuberosum* × *S. chacoense*. All other triploids had 10 trivalents or less (Table 7). The large

number of multivalents in the triploid hybrid *S. tuberosum* × *S. chacoense*, equaling that of *S. chacoense*, suggests a high degree of affinity among chromosomes of these two species. The other interspecific triploids, *S. stoloniferum* × *S. chacoense*,

Table 4. Analysis of variance for number of trivalents plus quadrivalents at M_I among triploid *S. chacoense* clones

Source of variation	df	SS	MS	F
Among clones	8	42.42	5.30	2.48*
Within clones	306	653.26	2.14	
Total	314	695.68		

*F. 05=1.94

Table 5. Analysis of variance of number of multivalents (III+IV) at M_I among triploids of interspecific crosses

Sources of variation	df	SS	MS	F
Among cross combination	5	2392.65	478.53	213.63**
Within cross combination	603	1524.98	2.24	
Total	608	3917.63		

**F. 01=3.02

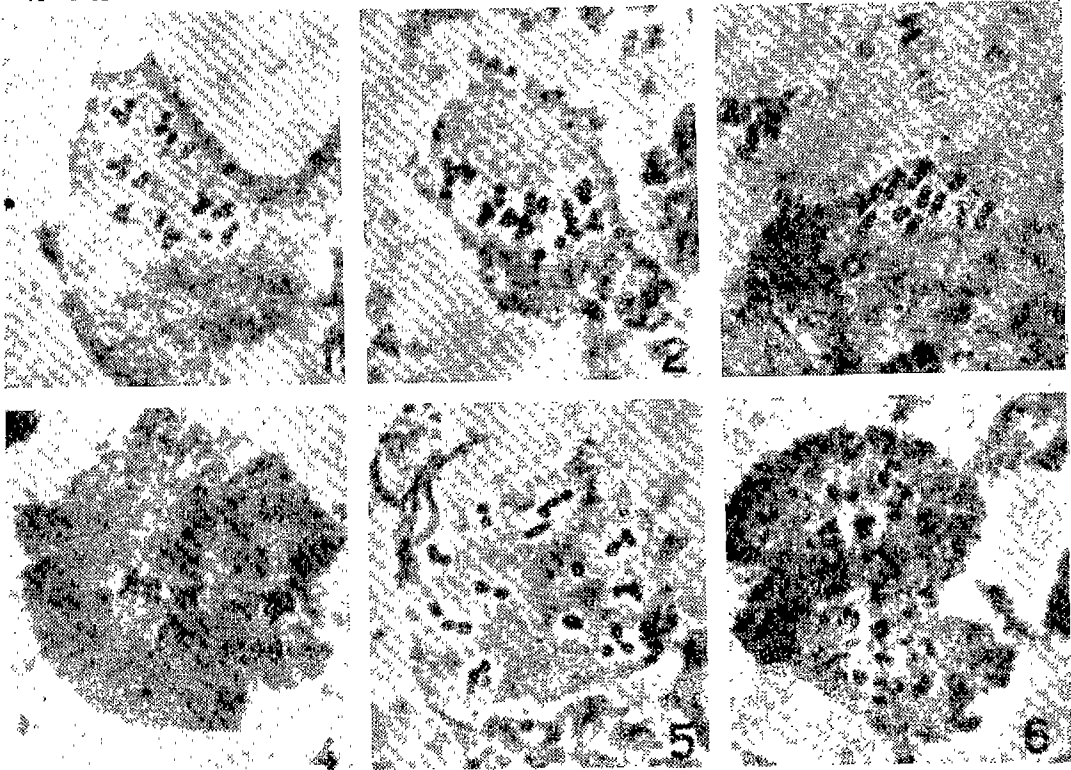


Fig. 1-6. Chromosome associations at metaphase I and chromosome distribution at metaphase II. 1. metaphase I in triploid 7-2 of *S. chacoense* with 6 trivalents+8 bivalents+2 univalents. 2. metaphase I in triploid 7-3 of *S. chacoense* with 8 trivalents+3 bivalents+6 univalents. 3. metaphase I in diploid *S. chacoense* 133124 with 12 bivalents. 4. metaphase I in tetraploid *S. chacoense* 189217 c. 18. with 2 quadrivalents+7 trivalents+8 bivalents+3 univalents. 5. metaphase I in triploid 65-9-1, hybrid of (*S. fendleri*×DH)×*S. chacoense* with 2 trivalents+13 bivalents+4 univalents. 6. metaphase II in triploid 8-2 of *S. chacoense* with 20:16 distribution.

Table 6. Pooled comparison of trivalents plus quadrivalents at Mi for each triploid type

Parents (4x×2x)	No. of cells	Mean No. of III+IV
<i>S. chacoense</i> × <i>S. chacoense</i>	315	8.25
<i>S. tuberosum</i> × <i>S. chacoense</i>	35	8.49
<i>S. stoloniferum</i> × <i>S. chacoense</i>	84	3.61
<i>S. stoloniferum</i> × <i>S. tuberosum</i>	70	4.29
<i>S. fendleri</i> × <i>S. tuberosum</i>	70	5.03
(<i>S. fendleri</i> × <i>S. tuberosum</i> (DH))× <i>S. chacoense</i>	35	4.86

Table 7. Frequency distribution of cells with various number of bivalents plus trivalents at Mi in triploids

Triploids		No. of II+III						Max. No. of III in a cell
		10	11	12	13	14	15	
<i>S. chacoense</i> × <i>S. chacoense</i>	freq.	0	6	274 ¹	32	2	1	12
	(%)	0	1.90	86.98	10.16	0.63	0.32	
<i>S. tuberosum</i> × <i>S. chacoense</i>	freq.	0	1	30	4	0	0	12
	(%)	0	2.86	85.71	11.43	0	0	
<i>S. fendleri</i> × <i>S. tuberosum</i> (DH) ²	freq.	0	2	49	18	1	0	9
	(%)	0	2.86	70.00	25.71	1.43	0	
(<i>S. fendleri</i> × <i>S. tuberosum</i> (DH))× <i>S. chacoense</i>	freq.	0	5	18	7	3	2	10
	(%)	0	11.43	54.29	20.00	8.57	5.71	
<i>S. stoloniferum</i> × <i>S. chacoense</i>	freq.	1	1	79	3	0	0	7
	(%)	1.19	1.19	94.05	3.57	0	0	
<i>S. stoloniferum</i> × <i>S. tuberosum</i>	freq.	0	0	70	0	0	0	7
	(%)	0	0	100.00	0	0	0	

1) include 8 cells with one quadrivalent

2) DH: cross, *S. phureja*×*S. tuberosum* haploid

S. stoloniferum×*S. tuberosum* and *S. fendleri*×*S. tuberosum* (DH), are presumably less closely related as they have fewer multivalent (Table 3 and 6).

A complex triploid involving three species had the maximum number of bivalent plus multivalent association in a given cell. Fifteen such associations were observed in 5.7% of the cells in the triploid of (*S. fendleri*×*S. tuberosum*(DH))×*S. chacoense* (Table 7 and Figure 5). Triploid hybrids between *S. tuberosum* and *S. chacoense*, and triploid *S. chacoense* showed an excess number of pairing (13 or more II+III+IV) in 11.43% and 11.11% of the cells respectively. Therefore a slight degree of autosyndesis does occur in these hybrids. However, such a low level does not necessarily support the suggestion that the basic chromosome number in potato is 6. The excess pairing might

be due to structural differences of chromosomes and eventually to non- or partial-homologous pairing. The relatively high percentage, 27.14, of cells with more than 13 bivalents plus trivalents in the triploid hybrids between *S. fendleri*×*S. tuberosum* (DH) and 34.28 in (*S. fendleri*×*S. tuberosum* (DH))×*S. chacoense* might indicate greater differentiation among these species.

Chromosome Distribution in Meiosis: Chromosome assortment in the first meiotic division is revealed by the metaphase II distribution (Table 8 and Figure 6). In a binomial distribution 18 chromosomes per cell would be most frequent. Indeed this is the most numerous class in most clones, however over-all distribution was skewed toward the lower numbers. This has been reported in other crosses (Kawakami and Matsubayashi, 1956) and might be due to irregular pairing behavior

Table 8. Frequency of chromosome number in metaphase II of meiosis for diploid, triploid and tetraploid

		Chromosome number									
		11	12	13	14	15	16	17	18	19	
Triploids											
<i>S. fendleri</i> ×	Freq.	0	0	3	0	9	31	38	53	25	
<i>S. tuberosum</i>	%	0	0	1.5	4.5	4.5	15.5	19.0	26.5	12.5	
<i>(S. fendleri</i> ×											
<i>S. tuberosum</i> (DH)) ×	Freq.	0	0	4	4	1	13	30	19	16	
<i>S. chacoense</i>	%	0	0	4.0	4.0	1.0	13.0	30.0	19.0	16.0	
<i>S. stoloniferum</i> ×	Freq.	0	2	4	7	38	71	133	158	85	
<i>S. chacoense</i>	%	0	0.4	0.7	1.2	6.7	12.6	23.6	28.0	15.1	
<i>S. stoloniferum</i> ×	Freq.	0	1	0	3	7	16	41	56	25	
<i>S. tuberosum</i>	%	0	0.6	0	1.8	4.2	9.6	24.7	33.7	15.1	
<i>S. tuberosum</i> ×	Freq.	0	0	3	1	10	10	23	31	11	
<i>S. chacoense</i>	%	0	0	3.0	1.0	10.0	10.0	23.0	31.0	11.0	
<i>S. chacoense</i> ×	Freq.	0	0	7	19	55	124	200	154	134	
<i>S. chacoense</i>	%	0	0	0.8	2.1	6.1	13.8	22.2	28.2	14.9	
Calculated freq.		0	0.2	0.3	1.6	5.4	12.1	19.3	22.6	19.3	
Diploid											
<i>S. chacoense</i>	Freq.	1	98	2	0	0	0	0	0	0	
P.I. 133124	%	1.0	98.0	2.0	0	0	0	0	0	0	
Calculated freq.		0	100	0	0	0	0	0	0	0	
Tetraploid											
<i>S. chacoense</i>	Freq.	0	0	0	0	0	0	0	0	0	
P.I. 1982.7 c. 18	%	0	0	0	0	0	0	0	0	0	
Calculated freq.		0	0	0	0	0	0	0	0	0	
		20	21	22	23	24	25	26	Total No. of cells	Ave. No. of lag.	Ave. No. of chrom. per cell
Triploids											
<i>S. fendleri</i> ×	Freq.	26	6	0	0	0	0	0	200	1.02	17.59
<i>S. tuberosum</i>	%	13.0	3.0	0	0	0	0	0			
<i>(S. fendleri</i> ×											
<i>S. tuberosum</i> (DH)) ×	Freq.	8	2	1	2	0	0	0	100	0.84	17.57
<i>S. chacoense</i>	%	8.0	2.0	1.0	2.0	0	0	0			
<i>S. stoloniferum</i> ×	Freq.	40	19	7	0	0	0	0	564	0.72	17.64
<i>S. chacoense</i>	%	7.1	3.4	1.2	0	0	0	0			
<i>S. stoloniferum</i> ×	Freq.	13	3	1	0	0	0	0	166	0.58	17.70
<i>S. tuberosum</i>	%	7.8	1.8	0.6	0	0	0	0			
<i>S. tuberosum</i> ×	Freq.	8	2	1	0	0	0	0	100	1.04	17.45
<i>S. chacoense</i>	%	8.0	2.0	1.0	0	0	0	0			
<i>S. chacoense</i> ×	Freq.	71	24	9	3	0	0	0	900	0.72	17.64
<i>S. chacoense</i>	%	7.9	2.7	1.0	0.3	0	0	0			
Calculated freq.		12.1	5.4	1.6	0.3	0.2	0	0			
Diploid											
<i>S. chacoense</i>	Freq.	0	0	0	0	0	0	0	100	0	12.00
P.I. 133124	%	0	0	0	0	0	0	0			
Calculated freq.		0	0	0	0	0	0	0			
Tetraploid											
<i>S. chacoense</i>	Freq.	0	0	6	26	52	13	3	100	0.38	23.81
P. I. 1982.7 c. 18	%	0	0	6.0	26.0	52.0	13.0	3.0			
Calculated freq.		0	0	0	0	100	0	0			

and elimination of lagging chromosomes. According to the chromosome distribution at M_{II} , gametes with balanced chromosome numbers (12 or 24) will be produced at a low frequency in triploids.

Chromosome distribution at M_{II} in diploid *S. chacoense* is regularly twelve, except for about one cell in fifty. In tetraploids of *S. chacoense* half of the cells had 24 chromosomes at M_{II} , the remainder were irregular because of univalent and trivalent formation at M_I .

Fertility: Triploids were very low in pollen fertility except in *S. tuberosum* × *S. chacoense* and triploid *S. chacoense* (Table 9). These had 49.16% and 30.25% stainable pollen respectively while the other triploids ranged from zero to less than 7.21%.

Since all triploids were similar in chromosome distribution at second metaphase (Table 8), the

difference in pollen fertility is probably not related to the balance in chromosome numbers. While the chromosome distribution at M_{II} is apparently not related to pollen fertility, chromosome affinity (pairing) at first metaphase (Table 3) is associated with fertility. The fertile triploids, *S. tuberosum* × *S. chacoense* and *S. chacoense* (3x), had a larger number of trivalents (7.60–8.69) compared with the others (2.57–5.51) (Table 3 and 9). This suggests that fertility in triploid hybrids might be more dependant on genome constitution than on chromosomal balance as Hermsen (1966) reported.

Equal or somewhat greater pollen viability was observed in triploid *S. chacoense* than in the tetraploid of that species (Lee, 1970). This further evidence that fertility is not necessarily related to the proportion of cells with balanced chromosome numbers.

Table 9. Pollen grain germination and stainability in tetraploids, triploids and diploids

Cross combination	% stained pollen-grains	No. of clones	% germ'd pollen-grains	No. of clones
Tetraploid				
<i>S. chacoense</i>	24.97	2	—	—
Triploid				
<i>S. stoloniferum</i> × <i>S. tuberosum</i>	1.33	4	0	1
<i>S. stoloniferum</i> × <i>S. chacoense</i>	1.93	6	0.10	2
<i>S. fendleri</i> × DH ¹	5.21	2	0.38	2
<i>S. tuberosum</i> × <i>S. chacoense</i>	49.16	1	—	—
<i>S. chacoense</i> × <i>S. chacoense</i>	30.25	9	—	—
Diploid				
<i>S. chacoense</i>	89.45	3	47.24	3
DH ¹	47.90	3	4.53	3

DH¹: cross, *S. phureja* female × *S. tuberosum* haploid male

CONCLUSION

All triploid hybrids studied average approximately twelve pairing (Bivalents plus multivalents) at meiosis. The number of bivalents, however, does not necessarily indicate affinity between parents as bivalents could arise from autosyndetic or allosyndetic pairing. Moreover, any set of 12

chromosomes is usually capable of pairing with any other set in tuber bearing *Solanum* species. The number of trivalents, however, should provide evidence of parental affinity.

Triploid hybrids of the interspecific cross *S. tuberosum* (4x) × *S. chacoense* (2x) had a large number of trivalents at meiosis, compared with other inter-specific triploid hybrids, and equalled 3x *S. chacoense*. These triploids also had greater

pollen fertility than the others. Evidently *S. tuberosum* and *S. chacoense* have a high degree of chromosomal homology. *S. fendleri* and *S. stoloniferum* are probably more distantly related to *S. tuberosum* and *S. chacoense*.

S. tuberosum in Series *Tuberosa* is thought to have originated in the Andes Mountains of northern South America. Its more primitive form, the tetraploid *S. andigena*, is geographically isolated from *S. chacoense*. The latter is native to lower elevation in south-eastern South America, principally in Argentina, and is included in Series *Comersoniana*. It is possible that these now allopatric species arose from a common ancestor is relatively recent times at some point in the central Andes.

S. fendleri occurs at the opposite extreme of the tuber-bearing *Solanum* range from *S. chacoense*, in Southwestern United States. Substantial chromosomal differentiation would be expected among them as a consequence of this extensive special isolation. The fact that such differentiation between *S. fendleri* and *S. tuberosum* is greater than between *S. chacoense* and *S. tuberosum* suggests either a relatively longer period of isolation between the northern and central range of tuber-bearing *Solanum* or the existence of more effective isolation barriers. The Isthmus of Panama with its humid tropical lowlands would constitute such a barrier. The complex triploid having one genome of each of these 3 species showed a pairing pattern similar to the *S. fendleri* × *S. tuberosum* triploid. Presumably the *tuberosum-chacoense* genomes tended to pair and the *fendleri* chromosomes persisted as univalents.

S. stoloniferum of Mexico is considered to be closely related to *S. fendleri*, both being in Series *Longipedicellata*. Recently it was shown to be an allotetraploid. When crossed with *S. chacoense* the derived triploids have the lowest trivalent incidence among those studies. Chromosomal affinity is slightly less than in the *S. stoloniferum* × *S. tuberosum* triploid. This, too, follows the pattern one might predict on the basis of geographic distribution.

The observed similarity in *chacoense* and *tuberosum* genomes should make cytological and genetic observation and inferences based on one species valid for the other as well. This is important in view of the expanding research on tuber-bearing *Solanum* species. Also, it is a simple matter to transfer genes between these species. Indeed, this inter-specific fertility raises doubts concerning the propriety of considering them as distinct species, in spite of their placement in separate series.

More than twelve pairings were observed in some triploid hybrid plants, indicating the presence of autosyndesis. This excessive pairing was assumed to be due to structural differences of chromosomes and eventually to non-or partial homologous pairing, since the maximum number of pairing in a given cell was present in a complex hybrid involving three species. Low pollen fertility in most triploids present difficulties in utilizing them for production of trisomic sets. This problem was not encountered in *S. chacoense*.

Since pollen increased in size with an increase in ploidy level, this should be useful in distinguishing ploidy among progeny of diploid-tetraploid crosses.

摘 要

4배체의 *S. tuberosum*, *S. stoloniferum*, *S. fendleri*, *S. chacoense*와 다른 2배체 種으로 만들어진 種間 혹은 種內 3배체 괴경형성 *Solanum* 雜種을 種間 간의 親和度를 연구하기 위하여 사용하였다. 3배체의 多價染色體의 수는 交配組合에 따라 달랐다. 그러나, *S. chacoense* 內에서 4x × 2x 교배에 의해 형성된 3배체는 *S. tuberosum* (4x) × *S. chacoense* (2x)의 교배에 의해 형성된 3배체와 비슷한 수의 多價染色體를 형성하였다. 많은 3배체 잡종이 약간의 同質接합을 하여 二價염색체와 三價염색체와 四價염색체를 합한수가 13 혹은 그 이상에 달하였다. 감자의 기본 염색체수는 12라 가정하여 약간의 파잉의 接합은 염색체의 구조적 차이, 결국에는 非相同 혹은 部分相同 染色體의 接합 때문이다 할 수 있다.

대부분의 三倍體雜種의 雄性稔성은 매우 낮으나(7.2%의 授精된 花粉) 예외로 *S. tuberosum* × *S. chacoense* 雜種 3배체와 *S. chacoense* 3배체는 授精된

화분의 비율이 각각 49.16%와 30.25%로 비교적 높았다. 花粉稔性は 제 2 中期의 열색체분포 보다는 제 1 종의 열색체의 親和度와 더 관련되어 있었다. *S. tuberosum* × *S. chacoense* 잡종 3배체의 많은 수의 多價染色體와 높은 花粉稔性は 이 두종의 친화도가 높다는 것을 제시하여 준다.

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(Received July 25, 1979)