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SPECIES DIFFERENTIATION IN *SOLANUM*, SECT. *PETOTA*

XI. Genomic Relationships between *S. acaule* and Certain Diploid *Commersoniana* Species

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Abstract

For assessing genomic relationships between a tetraploid species *S. acaule* (*acl*, $2n=48$) and two diploid *Commersoniana* (*COM*) species ($2n=24$), *S. saltense* (*slt*) and *S. schickii* (*sch*), cytogenetical behaviors were studied in triploid F_1 hybrids ($2n=36$) between them and also in amphiploids ($2n=72$) induced from the *acl* × *slt* hybrids.

Crosses were successful only when *acl* was used as the female parents, yielding germinable seeds of 86.4 and 98.2 per pollination in *acl* × *slt* and *acl* × *sch*, respectively. The triploid hybrids obtained with *slt* and *sch* showed mean pairing frequencies of $5.36_{III}+7.74_{II}+4.44_I$ (50 cells) and $5.59_{III}+7.11_{II}+5.00_I$ (64 cells) per cell at metaphase I, respectively, both with the modal configuration of $6_{III}+6_{II}+6_I$. Half of the cells or more had the sum of bivalents and trivalents in excess of the basic number of 12. Their occurrence is due possibly to intragenomic pairing. Such metaphase behavior resulted in the frequent occurrence of laggards at anaphase I, of scattered chromosomes at metaphase II and of micronuclei at sporadic stage. These hybrids were highly sterile in respect both to pollen and to seed, showing 2.7–4.8 of stainable pollen and producing a very few seeds only on backcrossing with the male parents. The *acl* × *slt* amphiploids showed very variable metaphase configurations, with a mean of $0.13_{VI}+0.02_V+5.93_{IV}+1.07_{III}+21.29_{II}+1.58_I$ (45 cells) per cell. The frequent formation of quadrivalents was particularly noted in this instance, their frequency per cell varying 3–9, with a mean of 5.93. During the subsequent stages the amphiploids behaved rather regularly to some extent, and they had 74.3% pollen fertility.

Based on the results obtained in this study and other available information, the following conclusion and a proposal were made : 1) the genome of diploid *COM* species is homologous with one of the *acl* genomes, and 2) *acl* is of segmental allotetraploid nature and assigned the genome formula of AAA^*A^* .

The problem of assessing genomic relationships in tuberous *Solanums* is of considerable importance for two reasons. First, it is a step towards understanding an aspect of species differentiation in this genus, and secondly, it may provide information useful in planning reasonable potato breeding programs which utilize many of the wild *Solanum* species known to possess valuable genes for improving potatoes.

Several triploid hybrids involving *S. acaule*

and diploid *Commersoniana* species have been already studied cytogenetically by some workers^{7,9,11}), and much has been described on their cytogenetical behavior. Our knowledge, however, seems to be not yet sufficient about the genomic affinity between the parental species in these hybrids. The same may also be said about a genome constitution of *S. acaule*.

Thus, this study was undertaken to bring such problems to a solution, using triploid F_1 hybrids obtained from the crosses, *S. acaule* × *S. saltense* and *S. acaule* × *S. schickii*, in which

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the male parents in each combination are diploid species of the *Commersoniana*, and also using amphiploid forms induced from the former hybrids. In this paper, the implications of the results obtained are discussed and, from this, a conclusive view will be given on the subjects not only of genomic relationships between the species involved but also of genome constitution of *S. acaule*.

Materials and Methods

The materials* used in this study were triploid F_1 hybrids obtained from crosses of the following tetraploid and diploid species and also amphiploids induced from one of these hybrids; *S. acaule* (*acl*), tetraploid species ($2n=48$) belonging to the taxonomic series *Acaulia* (ACA), supplied from the Inter-regional Potato Introduction Station, Wisconsin, U.S.A., with the accession number of P.I. 175396, and *S. saltense* (*slt*) and *S. schickii* (*sch*), diploid species ($2n=24$) both belonging to the series *Commersoniana* (COM), supplied from the same Station, with P.I. 189217 and 133720, respectively. Although both species have been included in *S. chacoense* by HAWKES³), their previous species names are used here for convenience.

Reciprocal crosses between *acl* and the two diploid species, *slt* and *sch*, were made under glasshouse conditions. Amphiploids were induced from some clones of the *acl* × *slt* hybrids by tuber treatment with colchicine. These

plants were all potted and grown in a glasshouse during the growing period from January to June. Meiotic configurations were analyzed in the P.M.C. squashes prepared by the acetocarmine technique modified by the present author¹⁰). Pollen preparations were made by staining with dilute acetocarmine solution and the percentages of well stained and normal-shaped grains were scored for estimating pollen fertility.

Results

Crossability

The results from reciprocal crosses between *acl* and the two diploid species are shown in Table 1. Crossability for each of the cross combinations was calculated by multiplying berry setting percentage, mean number of seeds per berry and germination percentage of seeds. Values calculated in this way may be available used in crossability comparison, since they represent the amount of germinable seeds per pollination. As seen from the table, crosses were successful only when *acl* was used as the female parents in either cases. Such a unilateral incompatibility as reported already by earlier workers^{2, 8, 12}) in the crosses involving *acl* was also found in the present instances. Crossability was of remarkably high order as compared with that of other tetraploid-diploid *Solanum* crosses⁹), indicating 86.4 and 98.2 in the crosses using *slt* and *sch* as the male parents, respectively.

Table 1. Results of interspecific crosses of *S. acaule* and diploid COM species

Cross combination	No. of flowers polli.	Berry setting			No. of seeds per berry		Seed germinability (%)	Cross- ¹⁾ ability
		No. of seedless berries	Seed-bearing berries					
			No.	%	Mean	Range		
<i>acl</i> × <i>slt</i>	20	0	20	100.0	131.9	69~200	65.5	86.4
Reciprocal	19	0	0	0	0	0	0	0
<i>acl</i> × <i>sch</i>	18	0	18	100.0	130.9	75~223	75.0	98.2
Reciprocal	23	0	0	0	0	0	0	0

1) For explanation, see text.

* The letters given in parentheses are the abbreviations of species and taxonomic series names, which have been proposed by SIMMONDS¹³).

Meiotic Behavior

Triploid hybrids

Meiotic configurations were analyzed at metaphase I in the two triploid hybrids, *acl* × *slt* and *acl* × *sch*. Diakinetic configurations were also analyzed in the latter hybrids. In Table 2 are given the mean frequencies and ranges per cell of univalents, bivalents and trivalents found in these materials, and in Figures 1a and b are shown two of the metaphase configurations observed. The two triploid hybrids were essentially similar to each other in pairing behavior, both showing 6_{III} + 6_{II} + 6_I as a modal pairing pattern at metaphase I. This pattern of pairing was encountered in 7 (14.0%) of the 50 cells examined for the *acl* × *slt* hybrids and 9 (14.1%) of the 64 cells for the *acl* × *sch*. Trivalent coefficient, i.e., percentage of the chromosomes participating in the trivalent formation, was assessed to be 44.67 and 46.51% in the *acl* × *slt* and *acl* × *sch* hybrids, respectively. Similarly high trivalent frequencies have been reported, as shown in Table 3, by earlier workers in all triploid involving *acl* and several other diploid *Solanums*, except the *acl* × *S. bulbocastanum* (*blb*) hybrids in which the rare occurrence of trivalents has been found by HERMSEN & RAMANNA⁶). The trivalent formation was also observed with a high frequency at diakinesis, verifying that the trivalents occurring in these triploid hybrids were formed by primary pairing but not by secondary pairing. Thus, triploid hybrids in-

volving *acl* and diploid species, apart from the *acl* × *blb* ones, seem to be characterized by the frequent formation of trivalents. The trivalents observed were mostly of V- and Q-shapes. They occurred in the form that two members participating in their formation are closely paired and the third is loosely connected with the pair. Other shaped ones were present only in occasional cells.

The configurations that the number of bivalents plus trivalents was more than the basic number of 12 were found in nearly half of the cells in both hybrids (Table 4), suggesting the occurrence of autosyndetic pairing within the basic set of 12 chromosomes, i.e. intragenomic pairing. The sum of bivalents and trivalents per cell in excess of 12 ranged from 13 to 17 and from 13 to 15 in the *acl* × *slt* and *acl* × *sch* hybrids, respectively. Fig. 1b shows one of such configurations, 13 being counted as the sum of paired chromosomes. A similar situation has been reported by several workers as presented in Table 3, in which 18 out of the 21 instances listed can be found to have the number of paired chromosomes in excess of 12 in mean frequency per cell.

Irregularities in metaphase pairing were followed by such irregular behaviors of the chromosomes at the subsequent stages as shown in Tables 5 and 6, and also in Figures 1c and d. At anaphase I, the triploid hybrids had lagging chromosomes in 52.0-67.2% of the cells, their mean numbers per cell being 1.07-1.22, with

Table 2. Chromosome pairing at diakinesis and metaphase I in two triploid hybrids and *acl* × *slt* amphiploids.

Hybrids	Meiotic stage	No. of cells observ.	Mean (± S.E.) and range (<i>Italic</i>) in number per cell ¹⁾					
			VI	V	IV	III	II	I
F ₁ , <i>acl</i> × <i>slt</i>	MI	50				5.36±0.26 (1~9)	7.74±0.46 (3~16)	4.44±0.39 (0~11)
	Diak.	35				6.49±0.24 (4~9)	6.31±0.34 (3~11)	3.91±0.22 (1~6)
F ₁ , <i>acl</i> × <i>sch</i>	MI	64				5.59±0.19 (3~9)	7.11±0.26 (3~11)	5.00±0.23 (1~8)
Amphiploid, <i>acl</i> × <i>slt</i>	MI	45	0.13±0.05 (0~1)	0.02±0.02 (0~1)	5.93±0.22 (3~9)	1.07±0.14 (0~3)	21.29±0.42 (15~27)	1.58±0.16 (0~5)

1) The symbols, I, II, III, IV, V and VI denote uni-, bi-, tri-, quadri-, penta- and hexavalent chromosomes, respectively.

the maximum of 5. No dicentric bridges with or without fragments were encountered in any case. At metaphase II, the chromosomes scattered outside the metaphase plates were found in 42.1–54.0% of the cells, with the mean numbers of 0.79–0.95 per cell, their maximum number being 4. Consequently, the numerically balanced plates with 12 chromosomes were found only in 0.5% of the plates

examined but those with 24 chromosomes were of no occurrence. Fig. 3 shows a comparison of the observed values with theoretical values expected from a binomial distribution, $(0.5 + 0.5)^{12}$, for chromosome distribution at metaphase II in the *acl* × *sch* hybrids. Although these two values being similar to each other in distribution pattern, the X^2 -test did reveal that significant differences exist between both,

Table 3. Metaphase I pairing frequencies reported by earlier workers for triploid hybrids from *S. acaule* × diploid *Solanums*

Male parent	Taxo- ¹⁾ nomic series	No. of cells observ.	Mean frequency per cell ²⁾				Refer- ence
			IV	III	II	I	
<i>S. chacoense</i>	COM	50		4.10	8.72	6.40	13)
„	„	100		6.04	5.99	5.90	7)
<i>S. saltense</i>	„	64		5.59	6.67	5.88	11)
<i>S. schickii</i>	„	64		5.47	6.88	5.83	„
<i>S. stenotomum</i>	TUB	100		5.16	7.20	6.12	„
„	„	21		7.40	5.20	3.70	4)
„	„	15	0.27	2.73	10.33	6.00	„
„	„	25		4.00	8.63	6.56	„
<i>S. phureja</i>	„	18		6.22	5.94	5.44	1)
„	„	100		6.30	5.71	5.68	7)
<i>S. rybinii</i>	„	21		3.90	9.24	5.81	1)
„	„	60		4.73	7.67	6.47	11)
<i>S. goniocalyx</i>	„	20		6.50	5.45	5.60	1)
<i>S. simplicifolium</i>	„	20		3.05	9.00	8.85	17)
<i>S. verrucosum</i>	„	80		5.71	6.54	5.79	11)
„	„	100		5.55	6.46	6.43	7)
Dihaploid							
<i>S. tuberosum</i>	„	82		3.25	8.81	8.58	6)
„	„	100		6.02	5.97	6.00	7)
<i>S. bulbocastanum</i>	BUL	23		0.39	12.30	9.91	6)
„	„	25		0.44	12.40	10.20	„
„	„	62		0.48	11.50	11.28	„

1) COM, TUB and BUL are the abbreviations of the taxonomic series, *Commersoniana*, *Tuberosa* and *Bulbocastana*, respectively.

2) For I, II, III and IV, see Table 2.

Table 4. Frequency of intragenomic pairing at metaphase I in two triploid hybrids

Hybrids	No. of cells observ.	Number of trivalents + bivalents per cell							
		10	11	12	13	14	15	16	17
F ₁ , <i>acl</i> × <i>slt</i>	50	1 (2.0)	3 (6.0)	21 (42.0)	7 (14.0)	9 (18.0)	3 (6.0)	4 (8.0)	2 (4.0)
F ₁ , <i>acl</i> × <i>sch</i>	64	0 (0)	3 (4.7)	26 (40.6)	25 (39.1)	7 (10.9)	3 (4.7)	0 (0)	0 (0)

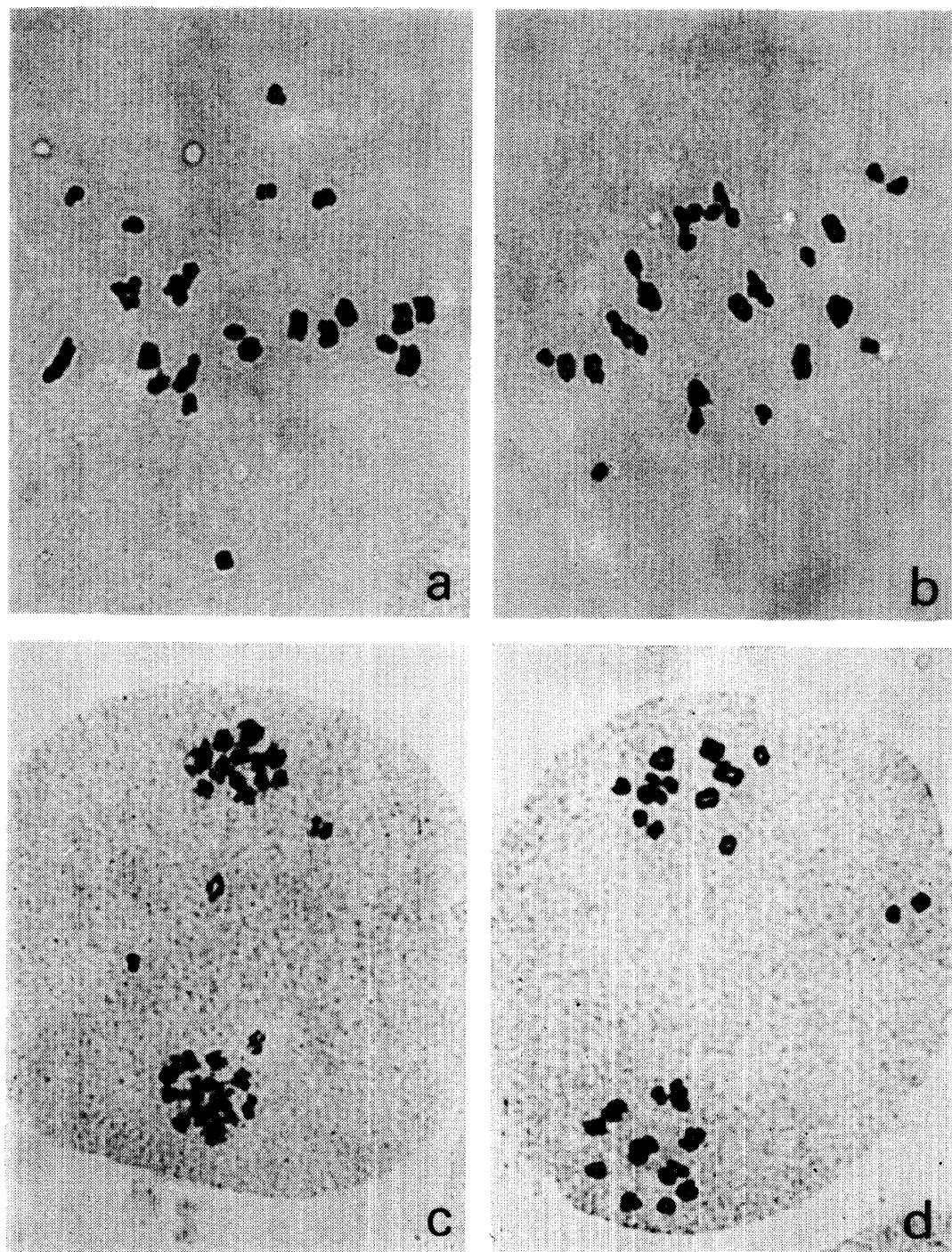


Fig. 1. Meiotic configurations in two triploid hybrids (ca. $\times 1800$)
 a. M-I in *acl* $\times$ *slt* hybrid, 5II+7I+7I; b. M-I in *acl* $\times$ *sch* hybrid, 6II+7I+4I;
 c. Late A-I in *acl* $\times$ *slt* hybrid, with 4 laggards; d. M-II in *acl* $\times$ *sch* hybrid, with
 2 scattered chromosomes.

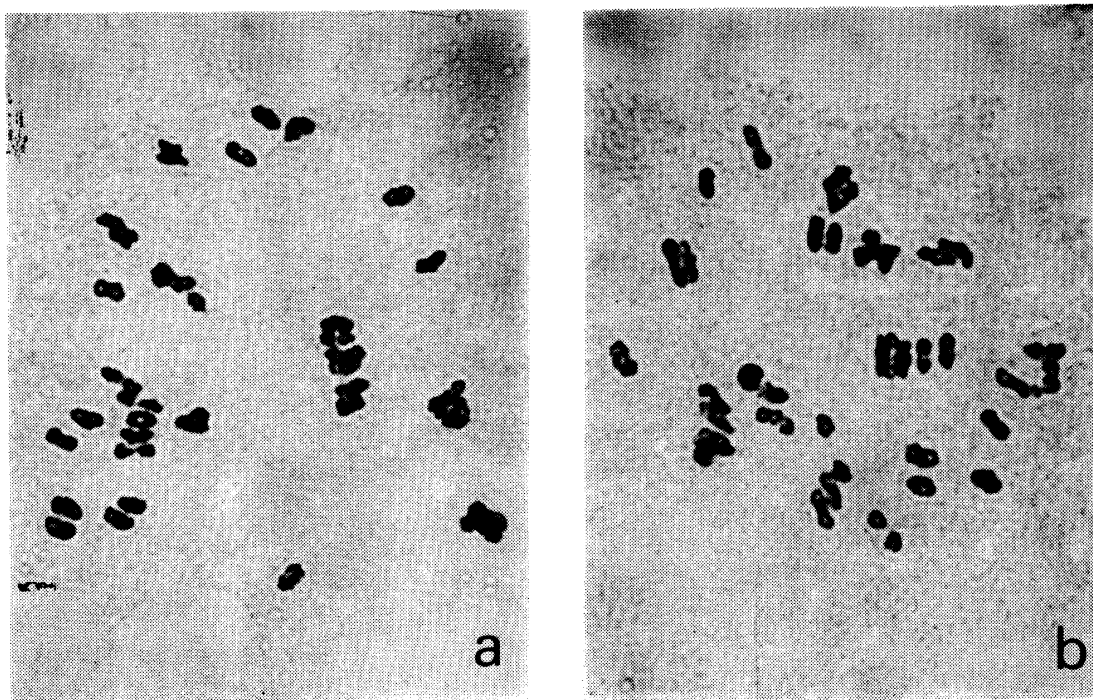


Fig. 2. Metaphase I configurations in the *acl* $\times$ *slt* amphiploids. (ca. $\times$ 1800)
 a. $5W+1U+24I+1I$; b. $1W+7W+19I$.

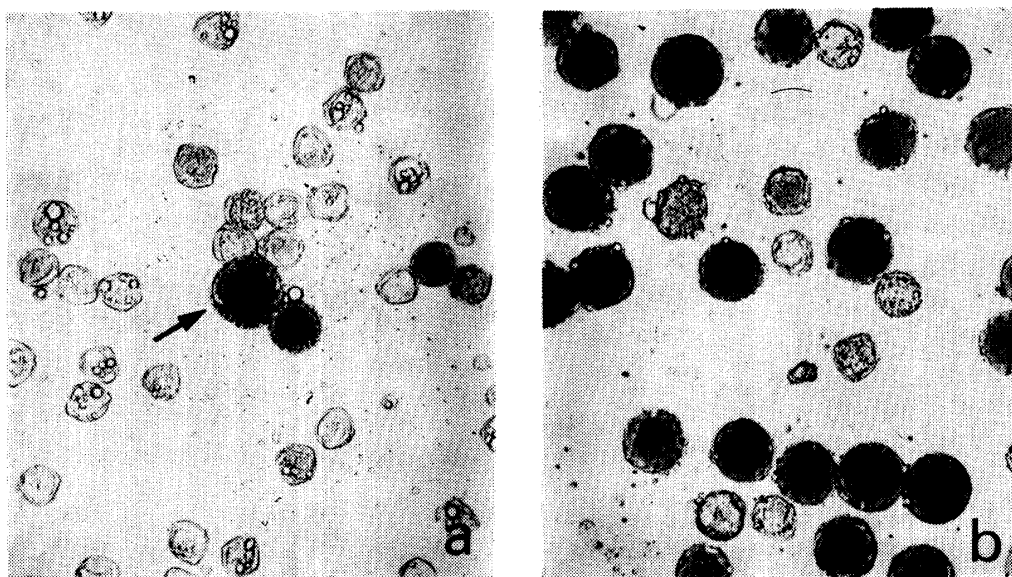


Fig. 3. Pollen grains of the *acl* $\times$ *sch* hybrid (a) and the *acl* $\times$ *slt* amphiploid (b). (ca. $\times$ 360)
 The arrow indicates an unreduced grain.

the observed values being above the expectation at the point of 12 chromosomes and below at the points of 21 and higher chromosomes. This appears to be due apparently to the occurrence of scattered chromosomes at metaphase II resulting from irregularities of chromosome behavior at earlier stages. This irregular distribution of chromosomes resulted in the formation of sporads containing several micronuclei. Of the sporads scored, 26-27% were tetrads with normal appearance. It is assumed from the above, however, that most of these tetrads may be composed of microspores with various unbalanced chromosome constitutions.

Amphiploids

The amphiploids induced from the *acl* × *slt* hybrids showed, as seen in Table 2, fairly

complicated meiotic configurations including, besides univalents, various paired chromosomes ranging from bivalents to hexavalents at metaphase I (Figs. 2a and b). Contrary to expectation, there were not detected the cells with regularly formed 36 $\parallel$ or similar pairing patterns but those with a considerable amount of quadrivalents. Pentavalents and hexavalents were also present in some cells. The modal configurations were 6 $\parallel$ +1 $\parallel$ +22 $\parallel$ +1 $\parallel$ and 5 $\parallel$ +2 $\parallel$ +22 $\parallel$ +2 $\parallel$, they each being observed in 8.9% of the cells examined. The frequency of quadrivalents counted was a mean of 5.93 per cell and varied from 3 to 9 among different cells. Such high quadrivalent frequencies have been previously observed by the present author¹⁾ for some amphiploids between *acl* and

Table 5. Chromosomes behavior at anaphase I in two triploid hybrids and *acl* × *slt* amphiploids

Hybrids	No. of cells observ.	Cells ¹⁾ with lag. (%)	No. of lag. ¹⁾ per cell		Bridges (%)
			Mean	Range	
F ₁ , <i>acl</i> × <i>slt</i>	500	52.0	1.07	0~5	0
F ₁ , <i>acl</i> × <i>sch</i>	464	67.2	1.22	0~5	0
Amphiploid, <i>acl</i> × <i>slt</i>	454	39.4	0.52	0~4	0

1) lag.: lagging chromosomes.

Table 6. Chromosome behavior at metaphase II and sporad stages in two triploid hybrids and *acl* × *slt* amphiploids

Hybrids	No. of cells observ.	Cells ¹⁾ with scat. (%)	Metaphase II				Sporad
			No. of scat. ¹⁾ per cell		No. of chromo- somes per plate		Normal pollen tetrad (%)
			Mean	Range	Range	Balanced (%) ²⁾	tetrad (%)
F ₁ , <i>acl</i> × <i>slt</i>	107	42.1	0.79	0~4	12~23	0.5	26.6
F ₁ , <i>acl</i> × <i>sch</i>	63	54.0	0.95	0~4	12~21	0.5	27.4
Amphiploid, <i>acl</i> × <i>slt</i>	104	40.0	0.54	0~3	35~38	47.1	58.8

1) scat.: scattered chromosomes.

2) The metaphase I plates consisting of 12 or 24 chromosomes for the triploid hybrids and 36 chromosomes for the amphiploids were scored as balanced.

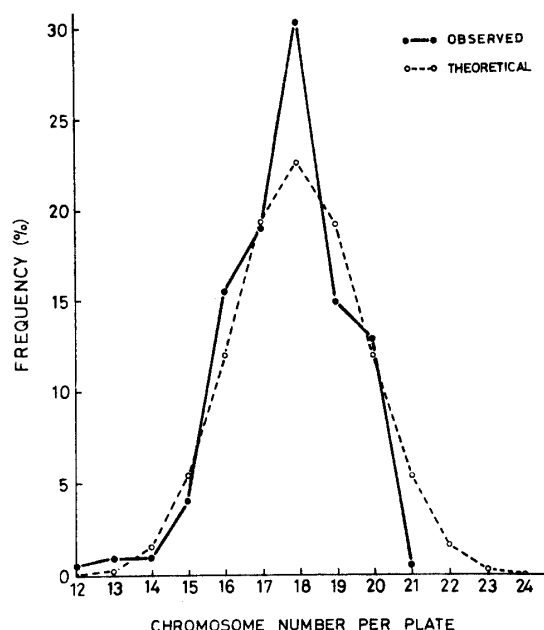


Fig. 4. Graph showing a comparison of the observed and theoretical frequencies in chromosome distribution at metaphase II in the *acl* × *sch* triploid hybrids.

other diploid *Solanums*, although SWAMINATHAN¹⁴⁾ and HERMSEN & RAMANNA⁶⁾ have reported no quadrivalent formation in the *acl* × *S. simplicifolium* (*sim*) amphiploids and rare occurrence of quadrivalents in the *acl* × *blb* amphiploids, respectively.

Compared with the triploid hybrids, the amphiploids showed a tendency to have less the irregularities in chromosome behavior at the subsequent stages (Tables 5 and 6). Laggards were seen with a mean frequency of 0.52 per cell in 39.4% of the cells, and about half of the metaphase II plates observed were

numerically balanced ones consisting of 36 chromosomes. Of the sporads counted, about 59% were normal tetrads and the remainings had one or more micronuclei.

Fertility

Triploid hybrids

Fertility estimates were made both from pollen grains and from ovules, and the results are given in Tables 7 and 8. Stainable and normal-shaped pollen grains were judged as fertile, and they were assorted depending on their sizes into three types, small, middle and large, which could be presumably regarded as being at ploidy levels corresponding to haploid, diploid and triploid, respectively. Large grains, therefore, may be regarded as unreduced ones when they would be found in the triploid hybrids. Pollen grains of the triploid hybrids were mostly abortive and only 2.7–4.8% appeared to be fertile (Fig. 3a). These values are comparable to those reported by other workers^{7, 14)} in similar hybrids. Ovule fertility was measured by the amount of seeds produced after backcrossing with the male parents as well as after sib-mating, but the triploid hybrids yielded a very few seeds only on backcrossing.

Amphiploids

The *acl* × *slt* amphiploids were highly fertile, showing 74% in pollen fertility (Tables 7 and 8, and also Fig. 3b) and producing 13.3 seeds per pollination on sib-mating. Similar results have been reported by SWAMINATHAN¹⁴⁾ who found 61% pollen fertility in the *acl* × *sim* amphiploids and by HERMSEN⁵⁾ who obtained 10.4 seeds per pollination by selfing the *acl*

Table 7. Pollen fertility in two triploid hybrids and *acl* × *slt* amphiploids

Hybrids	No. of grains observ.	Stainable and normal-shaped grains ¹⁾						Abortive grains		Pollen stain-ability(%)
		Small		Middle		Large				
		Scored	%	Scored	%	Scored	%	Scored	%	
F ₁ , <i>acl</i> × <i>slt</i>	1830	19	1.0	20	1.1	10	0.6	1781	97.3	2.7
F ₁ , <i>acl</i> × <i>sch</i>	1204	21	1.7	18	1.5	19	1.6	1146	95.2	4.8
Amphiploid, <i>acl</i> × <i>slt</i>	1136	4	0.3	20	1.8	820	72.2	292	25.7	74.3

1) Small, Middle and Large denote pollen grains which were assumed to correspond the ploidy levels of x, 2x and 3x, respectively.

Table 8. Seed fertility in two triploid hybrids and *acl* × *slt* amphiploids

Hybrids	Polli- ¹⁾ nation	No. of flowers polli.	Berry setting (%)	Mean no. of seeds	
				per berry	per polli.
F ₁ , <i>acl</i> × <i>slt</i>	Sib	21	0	0	0
	× ♂	25	8.0	1.5	0.12
F ₁ , <i>acl</i> × <i>sch</i>	Sib	20	0	0	0
	× ♂	29	6.9	1.0	0.07
Amphiploid, <i>acl</i> × <i>slt</i>	Sib	24	58.3	22.7	13.25

1) Sib : sib-mating, × ♂ : back-crossing with the male parents.

× *blb* amphiploids.

Discussion

Genomic Relationships between *S. acaule* and Diploid *Commersoniana* Species

For assessing interrelationships of the parental genomes, it is of course important to inquire into the origin of the paired chromosomes formed in the hybrids concerned. In this respect, the results obtained in the present triploid hybrids seem to be explained on either of the following two hypotheses. The first is based on the view that 12 chromosome pairs are formed by allosyndesis between one of the two gametic sets of *acl* genomes and a genome of the parental diploid species and trivalents occur from the associations of these 12 pairs with several chromosomes of another set of the *acl* genomes. On this view, the present author⁹⁾ has already explained homology relationships between the parental genomes in the triploid hybrids involving *acl* and certain diploid *Solanums*. The second takes, in contrast with the above, its basis on the view that the two sets of *acl* genomes do autosyndetically pair to form 12 chromosome pairs and the associations of these pairs with some chromosomes of the genome of parental diploid species result in the trivalent formation. From this point of view, an explanation has been attempted by HERMSEN & RAMANNA⁶⁾ for interpreting the pairing behavior exhibited by the *acl* × *blb* hybrids.

To decide which of these hypotheses is more probable for interpreting the meiotic configurations found in the present triploid hybrids, criteria are laid down from the following facts. 1) the triploid hybrids have significantly low trivalent frequencies as compared with autotriploid forms induced from certain diploid *Solanum* species; e.g. a triploid form of *S. verrucosum* has been reported to possess a mean of 10.28 ± 0.17 and a range of 7-12 in trivalent frequency per cell⁹⁾. This can be taken as evidence for indicating that the two sets of *acl* genomes are not so sufficiently homologous to form 12 chromosome pairs. 2) the *acl* × *slt* amphiploids form quadrivalents with an unexpectedly high frequency. The frequent occurrence of quadrivalent formation seems explainable only by presupposing the existence of high homology between one set of the *acl* genomes and the genome of diploid *COM* species, since it may be expected that the four somatic sets of *acl* genomes included in the amphiploids should, as a rule, behave in the same manner as in *acl per se* which has been found to form regularly bivalents only^{7,8,9)}. 3) many of the trivalents observed are formed in the form that, of the three chromosomes involved in a trivalent formation, one is paired loosely with other tightly paired chromosome, implying that such a loose pairing results from partial homology between the two gametic sets of *acl* genomes. 4) the chromosome distribution observed at metaphase II in the *acl* × *sch* hybrids is similar in its pattern to the theoretical distribution expected when the triploid hybrids

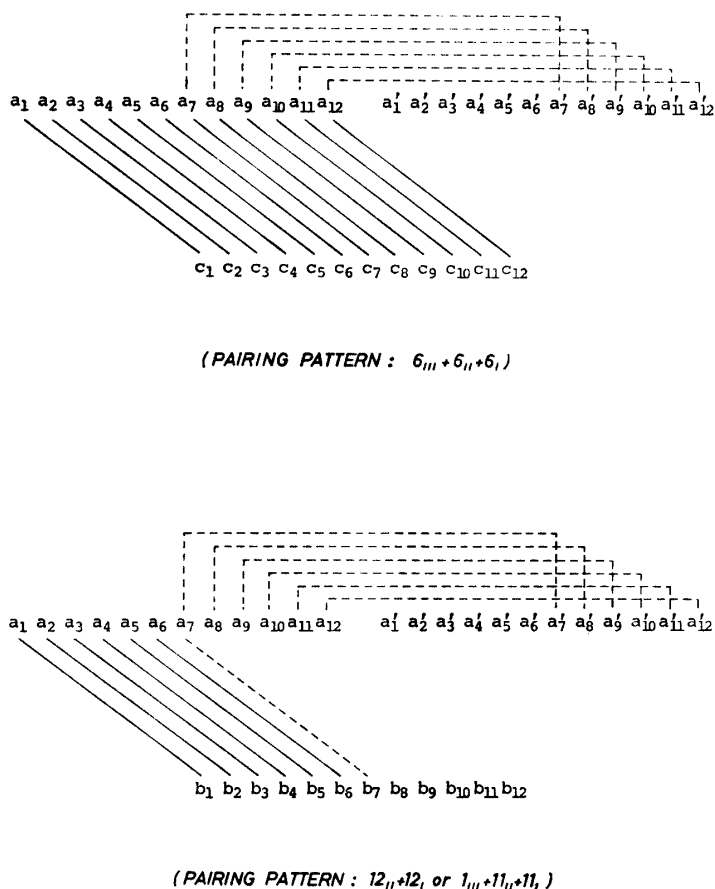


Fig. 5. Schemes illustrating probable modes of chromosome pairing in the meiotic configurations found in the present triploid hybrids (upper) and the *acl* × *blb* triploid hybrids (lower).
— : homologous, ---- : patially homologous.

carried at least two homologous genome sets.

Taking in account the above facts, the first hypothesis seems reasonable to explain the results obtained in this study. It is considered probable, therefore, to conclude that the genome of diploid *COM* species is homologous with one set of the *acl* genomes and that two sets of the *acl* genomes are partially homologous, thus confirming the view presented previously by the present author⁹⁾, although the final decision has to wait till meiotic pairing behavior is studied in dihaploid *acl*.

On the other hand, the meiotic configurations, which were characterized by the predominance of univalent and bivalent formation, found by HERMSEN & RAMANNA⁶⁾ in the *acl* × *blb* hybrids may be explained as follows : of the

chromosomes involved in one set of the *acl* genomes, several pair with those of the *blb* genome and remainings pair autosyndetically with several chromosomes of another set of the *acl* genomes. Fig. 5 illustrates schematically this situation. In this figure, 12 chromosomes from each of two sets of the *acl* genomes are designated as $a_1, a_2, \dots, a_{12}$, and $a'_1, a'_2, \dots, a'_{12}$ and those from each of the genomes of *blb* and diploid *COM* species as $b_1, b_2, \dots, b_{12}$, and $c_1, c_2, \dots, c_{12}$, respectively. If such a explanation is correct, it may be considered that the *blb* genome is less homologous with one set of the *acl* genomes than is the genome of diploid *COM* species.

Genome Constitution of *S. acaule*

It has been pointed out by many workers^{7,8,9,15)} that *acl* shows always regularly formed 24_{II} at meiosis and is highly fertile. This tetraploid species, so far as this is concerned, appears to be of allopolyploid nature. This species, however, exhibits a fairly high frequency of trivalent formation in the triploid hybrids with certain diploid *Solanums*, as seen from Tables 2 and 3. Such a frequent occurrence of trivalents does not seem able to be accounted for without assuming that autosyndesis might occur between the two gametic sets of *acl* genomes, and the occurrence of autosyndesis can be taken as an indication of homology existing between the genomes concerned. This homology, however, is in such a degree as mentioned in the preceding paragraph, indicating that the two sets of *acl* genomes are partially homologous with each other. This species, therefore, may be considered to be segmental allotetraploid, as suggested already by the present author⁹⁾, inasmuch as it represents a condition intermediate between the extremes of strict auto- and allopolyploidy.

For *acl*, various symbols have so far been proposed to designate its genomes; $A_2A_2A_3A_3$ by HAWKES³⁾, AAA^aA^a by the present author⁹⁾ and AAB^aB^a by IRIKURA⁷⁾. The reason why the present author used such a symbol was that this species is segmental allotetraploid and possesses a genome in common with diploid *COM* species, to which was assigned

the genome symbol AA. However, in view of the necessity to make a generalization of genome designation for tuberous *Solanums*, it is newly proposed here to alter the above genome symbol for *acl* to AAA^aAA^a.

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バレイショ近縁種における種の分化

XI. *S. acaule* と *Commersoniana* 群 2 倍種とのゲノム類縁関係

松 林 元 一

要 約

Acaulia 群所属の野生 4 倍種 *S. acaule* (*acl*, $2n=48$) と *Commersoniana* (COM) 群所属の野生 2 倍種 ($2n=24$), *S. saltense* (*slt*) 及び *S. schickii* (*sch*), とのゲノムの類縁関係を明らかにするために, 両群間 3 倍雑種 ($2n=36$) 及び *slt* を父本とした雑種から育成された複 2 倍体 ($2n=72$) の細胞遺伝学的行動を常法によって追究し, 次の結果を得た。

1) 両群間の交雑は *acl* を母本としたときのみ成功した。その交雑能力は比較的高く, 受粉花当りの発芽可能種子数で示して 86.4~98.2 であった。

2) *slt* 関与の 3 倍雑種は $5.36\text{III}+7.74\text{II}+4.44\text{I}$ (50細胞), *sch* 関与のそれは $5.59\text{III}+7.11\text{II}+5.00\text{I}$ (64細胞) の M-I 平均対合頻度を示し, いずれもそのモードは $6\text{III}+6\text{II}+6\text{I}$ であった。ここにみられる 3 価頻度は, 母本として関与している *acl* を完全な異質 4 倍性とみなした場合には余りにも高く, 反面 *Solanum* の同質 3 倍体のそれに比べると有意に低い値である。また両雑種とも, ゲノム内対合によって, 半数余の細胞が基本数 12 を超えた細胞当り対合数 (3 価 + 2 価) を示した。A-I 及び M-II では半数前後の細胞に不規則な染色体行動がみられ, その結果, 花粉稔性は 2.7~4.8%, 種子稔性は父本による戻交雑で 0.07~0.12 の低率であった。

3) *acl* × *slt* の複 2 倍体の M-I 平均対合頻度は $0.13\text{VI}+0.02\text{V}+5.93\text{IV}+1.07\text{III}+21.29\text{II}+1.58\text{I}$ (45細胞) で, 特に細胞当り 3~9 にわたる高頻度の 4 価形成が目立った。A-I 以後の染色体行動は比較的正常で, 74.3% の花粉稔性と同系交雑で 13.25 の種子稔性を示した。

4) 以上の結果から, 両群間のゲノム類縁関係と *acl* のゲノム構成について次のような推論が導かれた。

i) COM 群 2 倍種のゲノムは *acl* がもつ 2 組 (单相) のゲノムの一つと相同である。これは, 当 3 倍雑種にみられる対合の主体が両親ゲノム間の異親対合で起こり, 3 価形成は *acl* の 2 組のゲノム間の部分相同によるとの見解に基づく。ii) *acl* は, 上記の見解に基づき, 部分異質 4 倍性と考えられる。すでに COM 群 2 倍種は AA ゲノムをもつことが認められているので, *acl* のゲノム型は AAA^aAA^a とするのが妥当である。