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STUDIES ON THE SPECIES DIFFERENTIATION IN THE SECTION TUBERARIUM OF SOLANUM*

VI. Meiotic Behavior of Amphiploids from *Solanum longipedicellatum* × *S. chacoense* and its Bearing on Genomic Affinity between the Parent Species

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It has been suggested by STEBBINS (1950) that, in identifying genomes of closely related diploid species whose chromosome differences are so small as not to affect pairing, an available evidence is given from analysis of cytological behavior of amphidiploids induced from between them. HOWARD and SWAMINATHAN (1952) have pointed out that cytological method based on this suggestion can availably be used for tuberous *Solanum*. According to this method, several diploid species in the genus have, already, been studied by earlier workers (SWAMINATHAN, 1953 and SWAMINATHAN & HOWARD, 1953).

On the other hand, when genomic affinity is studied in F_1 hybrids between polyploids and diploids, or between the formers, it is of importance to determine whether the chromosome associations found in the hybrids are due to autosyndesis or allosyndesis, or both. This, however, is very difficult or almost impossible under the conditions that the materials are kept intact. In such case the method mentioned above also is very useful means.

In the earlier preliminary report, MATSUBAYASHI (1955 b) has discussed a mode of chromosome pairing observed in the triploid F_1 hybrid ($2n=36$) from *S. longipedicellatum* ($2n=48$) × *S. chacoense* ($2n=24$), on reference to the data on the cytological behavior of its doubled plant ($2n=72$), and suggested that the paired chromosomes may had been formed allosyndetically. Thereafter, this was confirmed by further examinations of the same amphiploid material, and the detailed results will be given in this paper.

CHROMOSOME ASSOCIATION AT FIRST METAPHASE

Meiosis was studied in the pollen mother cells. The acetocarmine techniques employed here are

the same as those described previously (MATSUBAYASHI, 1955a).

Since the meiotic configurations at first metaphase observed in 1955 had been too variable, careful observations for the same material were again done in the next year to make sure of it. The details of chromosome associations found in this stage are presented in Table 1.

From this table, it will be seen that the data obtained by both the observations in 1955 and 1956 are closely similar to each other. The meiotic configurations are characterized by that pairing frequencies show so divergent variation that their maxima are unable to be decided. There are not 36 bivalents formed regularly at all but various combinations of quadrivalents, trivalents, bivalents and univalents, their numbers per cell being 0-6, 0-6, 17-31 and 0-10 respectively. The mean pairing frequencies were calculated as $3.10 \text{ IV} + 3.17 \text{ III} + 22.80 \text{ II} + 4.50 \text{ I}$ in 1955 and as $2.72 \text{ IV} + 3.08 \text{ III} + 23.29 \text{ II} + 4.47 \text{ I}$ in 1956. Figures 1, 2 and 3 show certain configurations at this stage. For reference, a critical analysis of the chromosome associations at diakinesis also was done in several cells, and its result was found to be almost similar to those observed at first metaphase, even though it shows a slightly higher frequency of multivalents than in the latter. In any case, for considering genome constitution of this amphiploid plant, it should be noticed that such high multivalent frequency as is indicated as 3 quadrivalents and 3 trivalents in the mean number per cell is found and that primary associations of higher order than quadrivalent are never observed in any cell so far as the authors concerned.

Thus, the present material differs evidently from two other amphiploids with 72 somatic chromosomes, which have been induced from the triploid hybrids *S. acaule* ($2n=48$) × *S. phureja* ($2n=24$) and *S. acaule* × *S. simplicifolium* ($2n=24$) by BAINS (1951) and SWAMINATHAN (1954 a), and then found to form $35.92 \text{ II} + 0.16 \text{ I}$ and $35.8 \text{ II} + 0.4 \text{ I}$ at first metaphase by the same authors respectively.

* Contributions from the Laboratory of Plant Breeding, Hyogo Agricultural College, Sasayama, Japan. No. 28.

TABLE 1. Chromosome association at first metaphase

	1955					1956				
	Frequency per cell of				No. of cells	Frequency per cell of				No. of cells
	IV	III	II	I		IV	III	II	I	
Configuration	0	2	28	10	1	0	4	28	4	1
	0	4	27	6	1	0	6	25	4	1
	1	1	31	3	1	1	3	28	3	1
	1	4	25	6	1	1	4	24	8	1
	1	6	20	10	1	1	5	23	7	1
	2	1	30	1	1	1	5	25	3	1
	2	3	25	5	1	2	2	25	8	1
	2	3	26	3	1	2	2	27	4	1
	2	3	27	1	1	2	3	25	5	1
	2	4	22	8	1	2	3	26	3	1
	2	5	22	5	1	2	4	24	4	1
	3	1	28	1	1	2	5	22	5	1
	3	2	27	0	1	3	1	28	1	1
	3	3	23	5	1	3	2	24	6	1
	3	4	23	2	2	3	2	25	4	2
	3	5	21	3	1	3	2	26	2	2
	3	6	19	4	1	3	3	22	7	3
	4	2	21	8	1	3	3	24	3	4
	4	3	21	5	1	3	4	20	8	1
	4	4	19	6	1	3	6	19	4	1
	4	4	20	4	2	4	1	26	1	1
	4	5	18	5	1	4	2	21	8	1
	5	2	20	6	1	4	2	23	4	2
	5	2	21	4	1	4	3	22	3	1
	5	4	18	4	1	4	4	20	4	2
	6	0	21	6	1	4	5	17	7	1
	6	1	21	3	1	5	0	24	4	1
	6	3	17	5	1					
Total	93	95	684	135	30	98	111	853	161	36
M±m	3.10 ±0.29	3.17 ±0.28	22.80 ±0.69	4.50 ±0.55		2.72 ±0.23	3.08 ±0.23	23.69 ±0.42	4.47 ±0.33	

TABLE 2. Frequency of different types in quadrivalent formation

									Total
Freq.	31	36	7	6	60	19	25	7	191
%	16.23	18.85	3.66	3.14	31.41	9.95	13.09	3.66	

TABLE 3. Frequency of laggards at first anaphase

	Number per plate							Total
	0	1	2	3	4	5	6	
Freq.	42	24	20	7	12	2	3	110
%	38.18	21.82	18.18	6.36	10.91	1.82	2.78	

TABLE 4. Chromosome distribution at second metaphase

Chromosome numbers in sister plates	1955	1956	Total	%
36 — 36	4	15	19	22.09
37 — 35	3	10	13	15.12
38 — 34	1	3	4	4.65
36 — 1 — 35	1	8	9	10.47
37 — 1 — 34	1	5	6	6.98
38 — 1 — 33	1	2	3	3.49
39 — 1 — 32	1	2	3	3.49
35 — 2 — 35	1	6	7	8.14
36 — 2 — 34	2	4	6	6.98
37 — 2 — 33	2	2	4	4.65
35 — 3 — 34	0	1	1	1.16
36 — 3 — 33	0	1	1	1.16
37 — 3 — 32	0	1	1	1.16
34 — 4 — 34	1	2	3	3.49
35 — 4 — 33	1	2	3	3.49
36 — 4 — 32	1	1	2	2.32
34 — 6 — 32	0	1	1	1.16
Total	20	66	86	

TABLE 5. Frequency of chromosome number in second metaphase plates

	Number per plate								Total
	32	33	34	35	36	37	38	39	
Freq.	7	11	24	40	56	24	7	3	172
%	4.07	6.40	13.95	23.26	32.56	13.95	4.07	1.74	

As seen in Table 1, the frequency of bivalents varied widely ranging from 17 to 31. About one-third of the bivalents observed were of ring type paired closely by two chiasmata and the remainings were of rod-shape with single terminal or subterminal chiasma. In the trivalents V- and Y-shaped types were seen in most cells and three types of single chain, triangle and P-shape in a few cell. The quadrivalents were formed in various shapes. Their types and frequencies are given in Table 2.

CHROMOSOME BEHAVIOR AT THE SUBSEQUENT STAGES

The chromosome separation at first anaphase was considerably irregular in most cells, showing the lagging chromosomes ranged from 1 to 6 (Tab. 3 and Fig. 4). Dicentric bridges and acentric fragments were present rarely. A few cell showed first division restitution resulted from failure of chromosome separation at first anaphase.

At second metaphase, some chromosomes were

frequently scattered off both of the sister plates and hence the distribution of chromosomes became fairly irregular. The occurrence of these scattered chromosomes may be mainly attributed to non-orientation of the univalents at first metaphase and delayed separation of some of the bivalents at first anaphase. Of 86 cells studied, thus, only 19 (22.1%) had normal distribution 36-36. The chromosome numbers per plate varied from 32 to 39 and numerically balanced plates with 36 chromosomes amounted to over 32% of the plates examined (Tabs. 4, 5 and Fig. 5).

At second anaphase lagging of divided chromosomes also occurred often. Restitution nuclei having 72 chromosomes on each of sister plates were observed occasionally at this stage. The cells at second telophase exhibited frequently several micronuclei scattered around four daughter nuclei (Fig. 6).

The sporads observed comprise various kinds ranging from monads to decads and about 10% of them were normal tetrads (Tab. 6 and Fig. 7). The

TABLE 6. Sporang analysis

	Monad	Dyad	Triad	Tetrad	Pentad	Hexad	Septad	Octad	Nonad	Decad	Total
Freq.	1	1	1	11	21	36	25	12	6	2	116
%	0.86	0.86	0.86	9.48	18.10	31.04	21.55	10.34	5.17	1.72	

TABLE 7. Pollen analysis

		Stainable										Abortive	Total
		Normal form					Abnormal form						
		Giant	Large	Middle	Small	Total	Large	Middle	Small	Total			
May	Freq.	2	698	48	8	756	49	34	5	88	1508	2352	
	%	0.09	29.68	2.04	0.34	32.15	2.08	1.45	0.21	3.74	64.12		
July	Freq.	6	566	48	8	628	92	37	8	137	2324	3082	
	%	0.19	18.32	1.55	0.26	20.32	2.98	1.20	0.26	4.44	75.24		

formation of monads and dyads must be certainly due to restitution nuclei occurred during the course of first and second divisions.

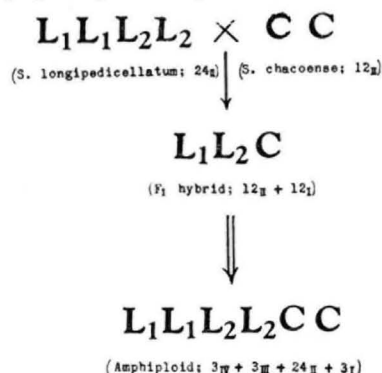
POLLEN FERTILITY

Pollen samples were prepared with dilute acetocarmine solution in both months of May and July and analysed in detail in order to ascertain good pollen ratio as indicated by their stainabilities, forms and sizes. The results are presented in Table 7. The stainable grains with normal form were assorted on the ground of their sizes into four classes: 'giant', 'large', 'middle' and 'small', their diameters being 35-42, 30-32, 26-28 and 20-24 in μ respectively. From a close similarity between the sizes of the three latter and those of pollen grains from naturally occurring hexaploid, tetraploid and diploid *Solanum* species, it may be suggested that the large, middle and small grains have the addition or loss of some chromosomes to or from the chromosome complements of 3x, 2x and x respectively, and that the giant grains have unreduced number resulted from restitution. Approximately 24 per cent on an average, thus, is a ratio of the good pollens produced naturally in the present amphiploid plant (Fig. 8).

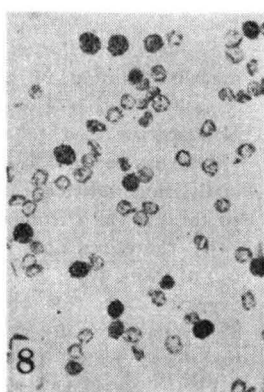
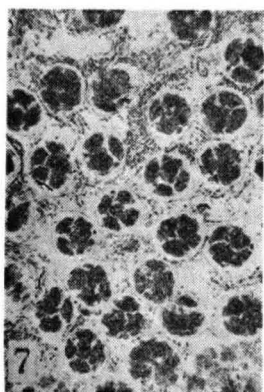
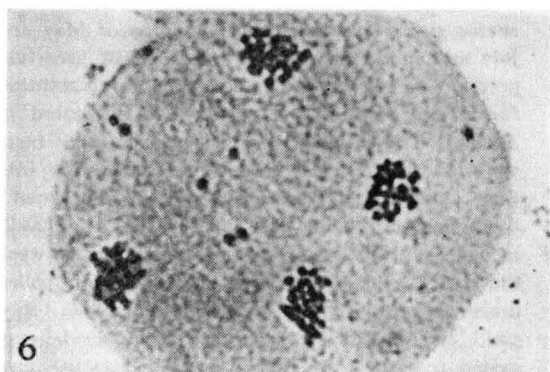
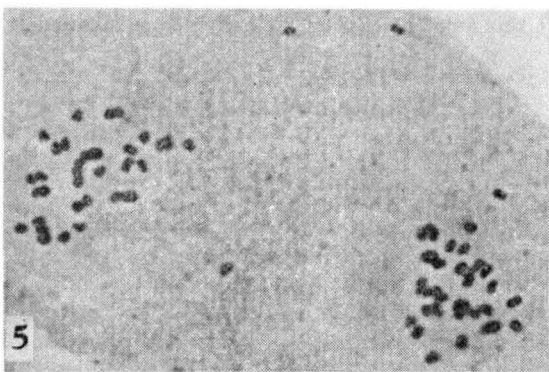
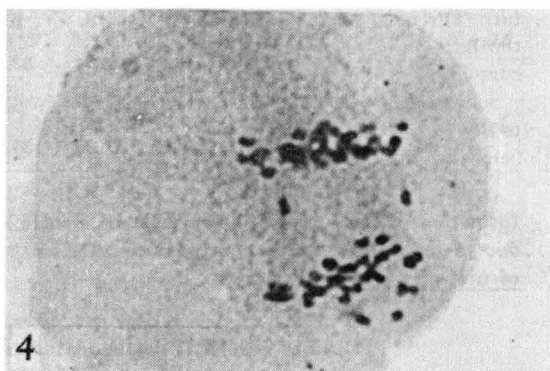
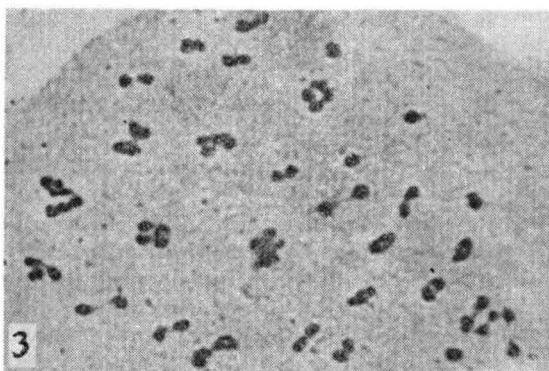
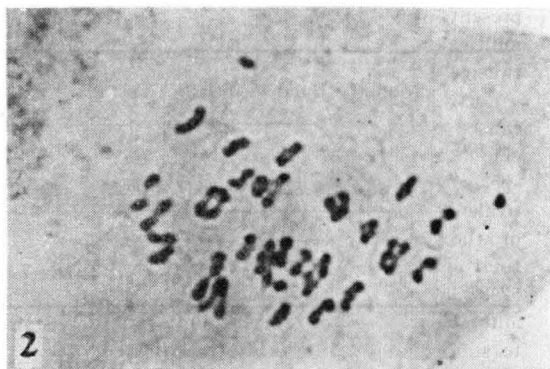
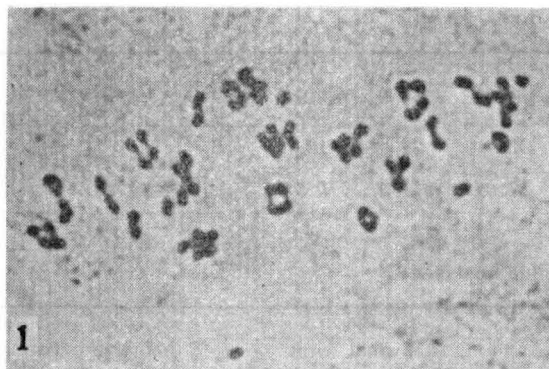
DISCUSSION

As mentioned above, unlike the two other doubled plants with 72 chromosomes from *S. acaule* $\times$ *S. phureja* and *S. acaule* $\times$ *S. simplicifolium*, the present material was found to have a significantly high multivalent frequency at first metaphase, showing three quadrivalents and three trivalents

in the mean number per cell. For considering a reason why it forms the multivalents in such a high frequency, the present authors will use here again the symbols for the chromosome sets which have been used in the previous reports (MATSUBAYASHI, 1955b and KAWAKAMI & MATSUBAYASHI, 1956). Thus, parentage and chromosome constitution of this amphiploid plant are presented as follows:



S. longipedicellatum is known to have regular meiosis, forming 24 bivalents at first metaphase (SWAMINATHAN, 1954 and MATSUBAYASHI, 1955a) and *S. chacoense* also to form 12 bivalents regularly (MATSUBAYASHI, 1955b). In the former species, especially, no multivalent formation has been observed so far. If the chromosome set (C) from *S. chacoense*, therefore, does not mate with either (L_1 or L_2) of those from *S. longipedicellatum*, it should be expected that this amphiploid plant shows only 36 bivalents usually at first metaphase, even though there are some irregularities in its pairing behavior. Nevertheless, there was in fact a high degree of the multivalent frequency. From this fact the



FIGS. 1, 2 and 3: First metaphase plates, with $6\text{IV} + 3\text{III} + 17\text{II} + 5\text{I}$, $6\text{IV} + 1\text{III} + 21\text{II} + 3\text{I}$ and $4\text{IV} + 3\text{III} + 21\text{II} + 5\text{I}$ respectively. FIG. 4: First anaphase, showing two laggards. FIG. 5: Second metaphase, showing 34-3-35 distribution. FIG. 6: Second telophase, having several scattered chromosomes. FIG. 7: Sporad stage, showing various polyads. FIG. 8: Pollen grains, indicating a low proportion of stainable ones.

(FIGS. 1 to 6: $\text{ca.} \times 1500$. FIG. 7: $\text{ca.} \times 250$. FIG. 8: $\text{ca.} \times 100$).

present authors are obliged to judge that the multivalent formation must have been made between CC and either L_1L_1 or L_2L_2 .

Furthermore, as seen from Table 8, this plant can be compared very advantageously with colchicine-induced autotetraploid forms of several related species in the frequency of multivalents. The multivalent coefficient, that indicates the percentage of the observed multivalents calculated on the total number of possible multivalents, is 48.38 and 52.22 in the present material and 49.65 in the autotetraploid *S. verrucosum* which has been known to show the highest multivalent frequency among the induced autotetraploid *Solanums* studied so far. The former's values are no less higher than the latter's one. This suggests that C is almost completely homologous with either L_1 or L_2 .

Such a interpretation would be further supported by the various irregularities of chromosome behavior at the subsequent stages, such as the

frequent occurrence of laggards at first anaphase, the low frequency of balanced plates at second metaphase, the frequent formation of several micronuclei at the sporad stage and the low percentage of pollen fertility. These irregular behaviors also have been found usually in some autotetraploid *Solanums* (MATSUBAYASHI, unpub.).

Taking these considerations into account, chromosome constitution of the amphiploid plant should be symbolized newly as LLCCCC instead of $L_1L_1L_2L_2CC$ that has been used previously. Hence this plant is regarded as a digenomous allohexaploid.

On the other hand, in the previous reports (MATSUBAYASHI, 1955b and KAWAKAMI & MATSUBAYASHI 1956), the authors have found that the triploid F_1 hybrid *S. longipedicellatum* $\times$ *S. chacoense* shows the mean pairing frequency of 12 bivalents plus 12 univalents at first metaphase. On the basis of the considerations mentioned above, it can be

TABLE 8. Comparison of multivalent frequency between the present material and several induced autotetraploid *Solanums*

Material	No. of cells studied	Number of quadrivalents + trivalents per cell										Mean per cell	Multiv. coefficient	Reference	
		0	1	2	3	4	5	6	7	8	9				
Present material	1955	30	—	—	2	1	2	5	4	8	4	4	6.27	52.22	Present study
	1956	36	—	—	—	—	5	10	14	3	2	2	5.81	48.38	
<i>S. rybinii</i> (4x)	20	—	—	1	4	6	5	3	1	—	—	—	4.40	36.67*	LAMM (1945)
<i>S. polyadenium</i> (4x)	25	—	—	—	3	4	5	5	4	4	—	—	5.56	46.67	SWAMINATHAN (1954)
<i>S. schickii</i> (4x)	75	4	14	10	22	12	6	6	1	—	—	—	2.95	24.56	MATSUBAYASHI (unpub.)
<i>S. verrucosum</i> (4x)	24	—	—	—	—	2	5	12	3	1	1	—	5.96	49.65	"

* Calculated by the authors from the original data.

concluded that 12 bivalents in this case were formed allosyndetically. Also, the same conclusion would be able to be applied to the case of the triploid F_1 hybrid *S. longipedicellatum* $\times$ *S. schickii*, in which $1_{III} + 11_{II} + 11_I$ have been observed by MATSUBAYASHI (1955a), for the reason that the pollen parents of both the F_1 hybrids have been ascertained to be completely homologous with each other in the genome constitution (MATSUBAYASHI, unpub.).

SUMMARY

In this paper, the meiotic behavior of an amphiploid plant with 72 somatic chromosomes,

induced from *S. longipedicellatum* $\times$ *S. chacoense*, is described and its significance to the genomic affinity between the parent species is discussed.

This plant shows such unexpectedly high multivalent frequency as is indicated as three quadrivalents plus three trivalents in a mean number per cell at first metaphase. The chromosome behavior during the subsequent meiotic course are considerably irregular, showing various abnormalities such as laggards at first and second anaphases, unbalanced plates at second metaphase, micronuclei in the sporads and pollen abortion.

From considerations on these behaviors, a suggestion is given as follows: 1) the genome of

S. chacoense is completely homologous with either of the two genomes of *S. longipedicellatum*, 2) thus, the genome formulae of LLCCCC for the amphiploid plant and LCC for both the triploid F₁ hybrids from crossing *S. longipedicellatum* with *S. chacoense* and *S. schickii* respectively are proposed anew. (Laboratory of Plant Breeding, Received Aug. 31, 1958),

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