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PDF issue: 2026-11-24

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(Citation)
兵庫農科大學研究報告. 農学編,2(2):143-148

(Issue Date)
1956

(Resource Type)
departmental bulletin paper

(Version)
Version of Record

(JaLCDOI)
https://doi.org/10.24546/81006524

(URL)
https://hdl.handle.net/20.500.14094/81006524

KOBE UNIVERSITY

STUDIES ON THE SPECIES DIFFERENTIATION IN THE SECTION TUBERARIUM OF SOLANUM

II. Meiotic Behaviour in the Triploid F_1 Hybrid from *S. longipedicellatum* × *S. chacoense*, with Some Regards to Chromosome Affinity between the Parent Species*

KOJIRO KAWAKAMI and MOTOKAZU MATSUBAYASHI

In polyploid species belonging to the section *Tuberarium* of *Solanum*, it is known that some of them, in spite of forming regularily only bivalents at the first meiotic metaphase in themselves, show, in their polyhaploid forms, a considerably high degree of pairing within their own gametic chromosome set (BAINS & HOWARD 1950, DODDS 1950, HOWARD & SWAMINATHAN 1953 and MARKS 1955). It is fairly difficult, therefore, to accurately elucidate whether the chromosome pairing found in the polyploid hybrids of *Solanum* is due to autosyndesis within the chromosome sets of one parent species or to allosyndesis between those of both parents. Thus this question has been pending for years.

To bring this problem to light is very important for researching the species differentiation in the genus.

Under such point of view, the present authors studied cytological behaviour of the triploid F_1 hybrid between *S. longipedicellatum* and *S. chacoense*, and attempted, based on this behaviour, some considerations on chromosome affinity between both the parent species. An outline of the results is given in this paper.

MATERIAL AND METHODS

The material used in the present study comprises F_1 hybrid ($2n = 36$) obtained by crossing *S. longipedicellatum* ($2n = 48$) with *S. chacoense* ($2n = 24$) and its parent species. They are the same as those employed in the previous study, in which those have morphologically been analysed (KAWAKAMI & TAKAYAMA 1955).

For analysing the meiotic configurations, while the pollen mother-cells were smeared with aceto-carmine solution, excellent slides favourable for the observations were obtained, after staining those materials for several days, by squashing in a drop of 45% acetic acid. The fertility of pollen from the matured anthers was examined in a dilute aceto-carmine solution.

* Contributions from the Laboratory of Plant Breeding, Hyogo Agricultural College, No. 19.

EXPERIMENTAL RESULTS

Sixty-three plates at the first meiotic metaphase in the F_1 hybrid *S. longipedicellatum* × *S. chacoense* were in detail analysed. The results are given in Table 1.

The meiotic configurations varied widely, showing various combinations of trivalents, bivalents and univalents. Besides 8–15 bivalents (mean 11.75) and 6–14 univalents (mean 10.27), in some cells a few trivalents (mean 0.75) occurred. This configuration, therefore, may be generalized as $1_{III}+11_{II}+11_{I}$ for the present (Fig. 3). On the other hand, considering that about one-fourth of PMC's observed shows $12_{II}+12_{I}$, it would also be possible to make this this configuration represent the pairing behaviour in the hybrid (Figs. 1 & 2). The very similar configuration has also been found in the F_1 hybrid from the cross *S. longipedicellatum* × *S. Schickii*, in which the male parent species belongs to the same taxonomic series *Commersoniana* that which S. *chacoense* belongs to (MATSUBAYASHI 1955a). In either case, primay associations of higher order than trivalent were never observed.

In the trivalent formation, there were both which are associated with two and three chiasmata, and their types, besides a triangle and a single chain type, were of V–, Y–, and P-shapes. In many cases, of three components taking part in the trivalent formation two are closely united with each other and another is loosely connected with the united one. The bivalent chromosomes consist of, besides some which are terminally or subterminally paired by single chiasma, those with two chiasmata terminalized well. Table 2 gives the chiasma frequency per bivalent and trivalent chromosome calculated at M-I in the hybrid. It is noticeable that most of them are more closely paired than in both the parents.

Moreover, it is remarkable that in about 43% of the cells observed the number of bivalents plus trivalents exceeds 12 (Tab. 1). Such meiotic configuration has also found in the F_1 hybrids from the crosses tetraploids × diploids in the different *Solanum*

Table 1. Chromosome association at lst meiotic metaphase

Configuration	Frequency per cell of III	II	I	No. of cells	%	Total number of III + II
	0	11	14	1	1.6	11
	0	12	12	16	25.4	12
	0	13	10	9	14.3	13
	0	14	8	2	3.2	14
	0	15	6	2	3.2	15
	1	11	11	7	11.1	12
	1	10	13	6	9.5	11
	1	13	7	1	1.6	14
	1	12	9	7	11.1	13
	2	10	10	5	7.9	12
	2	11	8	2	3.2	13
	2	12	6	4	6.3	14
	4	8	8	1	1.6	12
Total	47	740	647	63	100.0	
Mean ± m	0.75 ± 0.11	11.75 ± 0.16	10.27 ± 0.25			

Table 2. Chiasma frequency at lst meiotic metaphase

	Number of chiasmata 0	1	2	3	Total chiasmata	Total No. of chromo.	Chiasma freq.
Univ.	647	—	—	—	—	647	—
Biv.	—	410	330	—	1070	1480	1.45
Triv.	—	—	33	14	108	141	2.30



Fig. 1. First metaphase plate drawn separately, showing $12_{II}+12_{I}$, in the F_1 hybrid (× ca. 2500).

species (PROPACH 1937, KOOPMANS 1951, PRAKKEN & SWAMINATHAN 1952 and MATSUBAYASHI 1955a). This, as pointed out by the said investigators, may be probably due to a partial homology existing within the haploid set of 12 chromosomes.

During the first meiotic division the univalents behave at random. Out of the univalents, those which lie near the equator orientate themselves here during the anaphase and divide, formidg lagging chromosomes, and the other univalents pass towards the nearest pole undivided. Frequency of the laggards counted at A–I and T–I is shown in Table 3. In many cases, while the lagging univalents that failed to be included in both of the daughter nuclei are partly eliminated through the subsequent stages, the remainings surround themselves with their own nuclear membrane and form micronuclei with different size at the second telophase (Fig. 5).

At M-II the chromosomes per plate were observed in a varying number (Tab. 4 & Fig. 4). The numbers range from 12 to 21 with a mean of 16.48, showing very a few balanced plate having 12 chromosomes (1.2%). In triploid plants with 36 chromosomes, as a rule, the chromosome numbers at M-II might be expected to vary between 12 and 24 with a maximum at 18 according to a binomial distributon. This deviation from the expected random distribution is certainly due to the irregular behaviour of the lagging chromosomes mentioned above.

At the sporad stage, besides 4 tetrads with abnormal form, 27 pentads, 92 hexads, 78 septads, 29 octads and 6 novads were counted in a total of 236 cells examined (Fig. 6). Dyads and triads were not found at all.

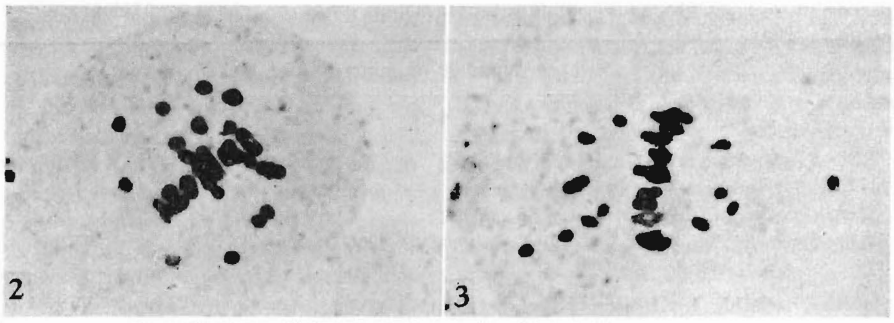


Fig. 2 and **3.** First metaphase plates in the F_1 hybrid, showing $12_{II}+12_{I}$ and $1_{III}+11_{II}+11_{I}$ respectively (× ca. 2000).

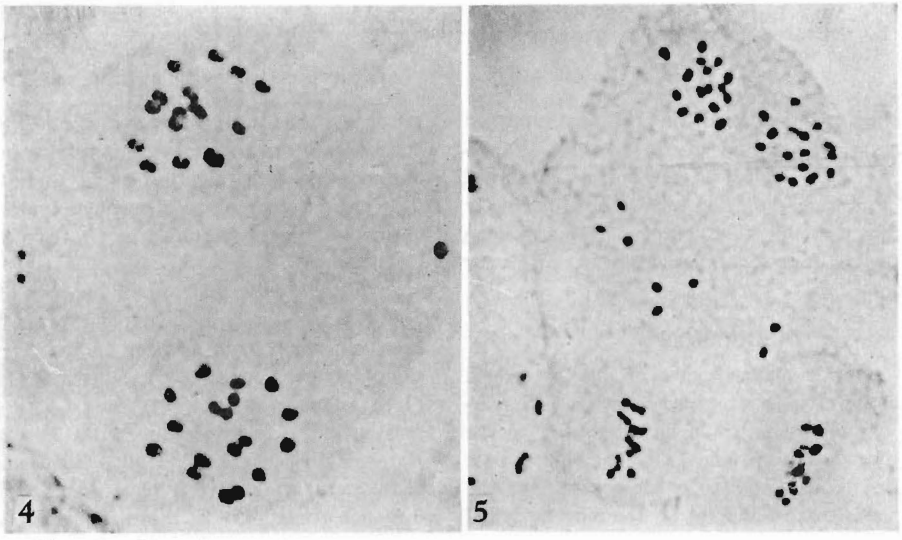


Fig. 4. Second metaphase in the F_1 hybrid, 18–2–16 distribution. (× ca. 2000).

Fig. 5. Second anaphase in the F_1 hybrid, showing 8 scattering monads (× ca. 2000).

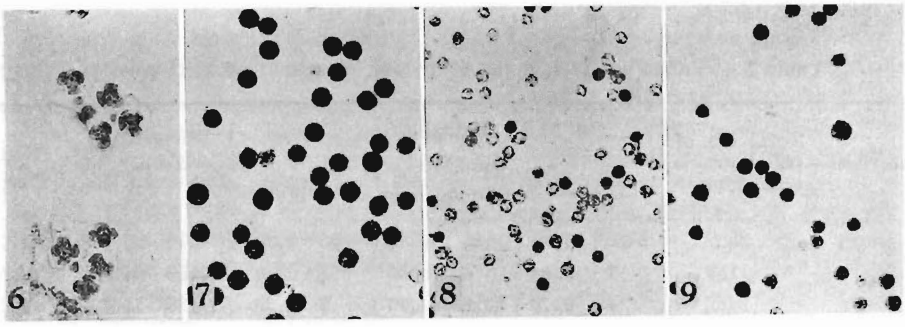


Fig. 6. Sporads taken to pieces by squashing. **Figs. 7, 8** and **9.** pollen grains of *S. longipedicellatum*, F_1 and *S. chacoense* respectively (× ca. 140).

Table 3. Frequency of lagging chromosomes at lst anaphase and telophase

No. of cells studied	Number of laggards per cell									M ± m
	0	1	2	3	4	5	6	7	8	
81	5	10	19	20	8	11	6	1	1	3.04 ± 0.19
	6.2	*12.3*	*23.5*	*24.7*	*9.9*	*13.6*	*7.4*	*1.2*	*1.2*	

(Italic figure: %)

Table 4. Chromosome distribution at 2nd meiotic metaphase

No. of plates studied	Chromosome numbers per plate										M ± m
	12	13	14	15	16	17	18	19	20	21	
162	2	4	13	24	41	32	30	10	4	2	16.48 ± 0.13
	1.2	*2.5*	*8.0*	*14.8*	*25.3*	*19.8*	*18.5*	*6.2*	*2.5*	*1.2*	

(Italic figure: %)

The pollen grains of the F_1 hybrid were analysed in comparison with those of its parents (Tab. 5 and Figs. 7,8 & 9). Most of the pollens examined consist of grains irregular in outline or imperfectly filled though stainable, and empty. Good pollens seeming to be functional, accordingly, are very rare (0.05%).

DISCUSSION

Of 36 somatic chromosomes of the F_1 hybrid plant from the cross *S. longipedicellatum* × *S. chacoense*, 24 chromosomes would be attributed to the tetraploid female parent and 12 to the diploid male parent. This is also able to be supported from the results of comparative studies on the morphological characteristics in the materials concerned (KAWAKAMI & TAKAYAMA, 1955).

In order to consider a chromosome affinity between both the parent species, it is very important to be sure of the composition of the paired chromosomes in the meiotic configurations $12_{II}+12_{I}$ or $1_{III}+11_{II}+11_{I}$ observed in the F_1 hybrid. For this purpose, it has to be considered whether the bivalent formation is due to autosyndetic pairing between two chromosome sets (signified as L_1 and L_2) from *S. longipedicellatum* or to allosyndetic pairing between chromosome sets (signified as C) from *S. chacoense* and L_1 or L_2.

Autosyndetic pairing in species hybrids of *Solanum*, especially in the triploid forms, has already been reported by, in addition to the workers mentioned above, EMME (1936), SCHWARZ (1937), OLÁH (1938), IVANOVSKAJA (1941) and LAMM (1945). In polyhaploid *S. demissum* with 36 chromosomes BAINS & HOWARD (1950), DODDS (1950) and HOWARD & SWAMINATHAN (1953) have found 4.7, 5.6 and 6.6~9.8 (max. 12) in the mean numbers of bivalents per cell respectively, and in polyhaploid plant with 24 chromosomes from *S. polytrichon* belonging to the same taxonomic series as *S. longipedicellatum*, MARKS (1955) has observed a mean bivalent frequency of 7.9 with a maximum at 12.

According to such data, it is presumed, in polyploid species of *Solanum*, that the greater

Table 5. Pollen analysis in the F_1 hybrid, compared with its parents

Materials	Total No. of pollen grains examined	Stainable						Empty		Pollen fertilty
		Normal*				Abnormal				
		A		B						
S. longi.	2557	2130	*83.31*	28	*1.09*	85	*3.32*	314	*12.28*	*84.40*
F_1	11159	1	*0.01*	4	*0.04*	598	*5.36*	10556	*94.60*	*0.05*
S. chaco.	2452	4	*0.16*	2316	*94.45*	7	*0.29*	125	*5.10*	*94.61*

* A is distinguished from B in the pollen size, being respectively 28~30 and 20~25 in diameter. (Italic figure: %)

part of the chromosomes within two or three sets are intergenomatically capable of pairing. If this is applicable to the pairing behaviour in *S. longipedicellatum* 12 bivalents in the present hybrid seem to be mostly attributable to autosyndetic pairing between L_1 and L_2 from the female parent.

However, even if these bivalents might be formed by pairing between L_1 and L_2, they must be more loosely paired, because no multivalent formation has been found at M-I in *S. longipedicellatum* itself (SWAMINATHAN 1954 and MATSUBAYASHI 1955 a). For such the present authors' view, an evidence is given from comparison between *S. demissum* and its polyhaploids in regard to their chiasma frequency per bivalent at M-I, i.e. 1.86 in the former that were calculated based on the data of SWAMINATHAN & Hougas (1954) and 1.16 in the latter based on the number per cell of rod and ring bivalents observed by HOWARD & SWAMINATHAN (1953). In other words, the bivalents in the polyhaploids show considerably looser pairing than in their original plants. Thereupon, the chiasma frequency calculated in the present F_1 hybrid shows 1.45 in the bivalents and 2.30 in the trivalents (Tab. 2). This comparatively high value seems to be what can not be expected by any possibility from chromosome pairing betweeen L_1 ane L_2.

Besides, at M-I in a amphidiploid *S. longipedicellatum-chacoense* ($L_1L_1L_2L_2$ CC) trivalents and quadrivalents have unexpectedly been observed with a high frequency (MATSUBAYASHI, 1955 b). Considering the fact that at M-I in *S. longipedicellatum* ($L_1L_1L_2L_2$) shows no multivalent formtion, their trivalents and quadrivalents must be due to chromosome association made between CC from *S. chacoense* and either L_1L_1 or L_2L_2 from *S. longipedicellatum*.

Based upon the last mentioned data, it would be more probable to interpret that the paired chromosomes in the F_1 hybrid were mostly made by allosyndetic pairing between L_1 and C, or L_2 and C, and partly by autosyndetic pairing between L_1 and L_2. If this is true, the formation of 12 bivalents in the *longipedicellatum-chacoense* hybrid would suggest that both of the parent species are closely related to each other by holding in common a very similar or an identical one set of 12 chromosomes.

SUMMARY

1) In this paper, the meiotic behaviour in the F_1 hybrid (2n=36) from the cross *S. longipedicellatum* (2n=48) × *S. chacoense* (2n=24) was described with special reference to the chromosome affinity between the parent species.

2) At the first metaphase in the hybrid $12_{II} + 12_I$ were observed as the most usual configuration, with some exception of showing a few trivalents besides bivalents and univalents. The hybrid showed various meiotic irregularities at the first anaphase and subsequent stages, and almost complete sterility.

3) Based on the available data, it was provisionally concluded that most of the paired chromosomes in the hybrid may be formed by allosyndetic pairing between the chromosome sets of the parent species, and that, accordingly, this behaviour suggests that one set of 12 chromosomes in each of *S. longipedicellatum* and *S. chacoense* may be very similar or identical to each other.

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