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Kawakami, Kojiro

Matsubayashi, Motokazu

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

V. Genomic Affinity between *Solanum verrucosum* and *S. demissum*

Kojiro KAWAKAMI and Motokazu MATSUBAYASHI

The taxonomists have classified *Solanum verrucosum* ($2n=24$) and *S. demissum* ($2n=72$) in the same taxonomic series of the section *Tuberarium* of the genus *Solanum; i.e.* BUKASOV (1938) and HAWKES (1944, 1956) have assigned these species to the series *Demissa* and CORRELL (1952) to the *Tuberosa*.

No matter to which series these species belong, morphologically *S. verrucosum* is very similar to *S. demissum*. In view the fact that the former is the only diploid species within the series *Demissa*, MARKS (1955) considered it to be "a possible ancestral diploid species" of hexaploid *Demissa*-species.

On the other hand, cytological study on the relationship between both the species has only been done by PROPACH (1937) up to the present. He who observed the F_1 hybrid from the cross *S. demissum* x *S. verrucosum* to show 24 bivalents at the first metaphase in several cells, suggested that the parent species are closely related by one very similar genome to each other.

The present work was undertaken with the purpose of identifying ancestral species making up *S. demissum*. In this paper, cytological observations made in the tetraploid F_1 hybrids from *S. verrucosum* × *S. demissum*, with special regards to genomic affinity between the parents will be given.

MATERIAL AND METHODS

Two plants with 48 somatic chromosomes obtained from crossing *S. verrucosum* ($2n=24$) with *S. demissum* ($2n=72$) as male parent were used in this work. It was morphologically ascertained that they were true hybrid between both the parents. The former parent species had been supplied through the Inter-regional Potato Introduction Station at Sturgeon Bay, Wisconsin and the latter from the Max-Planck-Institut für Züchtungsforschung, Voldagsen. In the cross *S. demissum*×*S. verrucosum* 35 pollinated flowers gave two small berries containing only shrivelled seeds, whereas in its reciprocal cross 20 pollinated ones produced 16 berries, two which set each one full-filled seed. Two seeds germinated well and gave rise to healthy plants.

The acetocarmine technique modified by MATSUBAYASHI (1955) was employed for making the meiotic preparations in the pollen mother cells. Pollen grains were stained with a dilute acetocarmine solution.

EXPERIMENTAL RESULTS

General course of meiosis in the hybrid plants used in this study was considerably regular. As seen in Table 1, observations on 72 plates at the first metaphase gave, on a mean pairing frequency, $0.81_{IV}+0.42_{III}+21.21_{II}+0.89_{I}$, with the maximum at 24_{II} and $1_{IV}+22_{II}$. Their configurations are shown in Figs. 1 and 2. This calculation does not exactly agree with that of PROPACH (1937), who has found the mean pairing frequency of $1.96_{IV}+0.9_{III}+17.64_{II}+2.48_{I}$ at the first metaphase in a similar material. The meiotic configuration in the present materials is evidently characterized by a lower frequency of univalents, in comparison with that found in the tetraploid F_1 hybrids from crossing *S. demissum* with several different diploid *Solanums* as will be given below.

Male parent	Mean freq. of univalents	Reference
S. caldasii	1.75	KOOPMANS (1951)
S. chacoense	2.36	MATSUBAYASHI (unpub.)
S. commersonii	5.26	KOOPMANS (1951)
S. rybinii	4.66	BAINS (1951)
〃	1.84	HOWARD & SWAMINATHAN (1952)
S. toralapanum	5.7	BAINS (1951)

(These values were calculated by the present authors from the original data.)

In the present hybrids, although the univalent frequency ranged 0 to 4, cells having no univalent amounted to 48.6% of ones examined (Table 2).

Such fewer occurence of univalents would be regarded as indicating how strong affinity exists between chromosome sets of both the parent species.

The bivalent chromosomes comprise two types; rod ones that are loosely paired by single terminal or subterminal chiasma and ring ones that are closely paired by two chiasmata. The frequency of the latter was found to be 7.88, this amounting

* Contributions from the Laboratory of Plant Breeding, Hyogo Agricultural College, Sasayama, Japan. No. 24.

Table 1. Chromosome association at M-I in the hybrids.

Configuration	Frequency per cell of IV	III	II	I	No. of cells	%
	0	0	24	0	13	18.1
	1	0	22	0	13	18.1
	1	1	20	1	8	11.1
	2	0	20	0	8	11.1
	0	1	22	1	6	8.3
	0	0	23	2	5	6.9
	1	0	21	2	5	6.9
	2	1	18	1	3	4.2
	1	1	19	3	2	2.8
	2	0	19	2	2	2.8
	1	2	18	2	2	2.8
	0	0	22	4	1	1.4
	0	2	21	0	1	1.4
	0	2	20	2	1	1.4
	0	2	19	4	1	1.4
	2	1	17	3	1	1.4
Total	58	30	1535	64	72	
M±m	0.81±0.09	0.42±0.07	21.32±0.22	0.89±0.13		

Table 2. Frequency of univalents at M-I in the hybrids.

	Number per cell 0	1	2	3	4	Total
Freq.	35	17	15	3	2	72
%	48.6	23.6	20.8	4.2	2.8	

Table 3. Frequency of ring bivalents at M-I in the hybrids.

Number per cell 5	6	7	8	9	10	11	12	Total	Mean
3	17	13	14	11	8	4	2	72	7.87

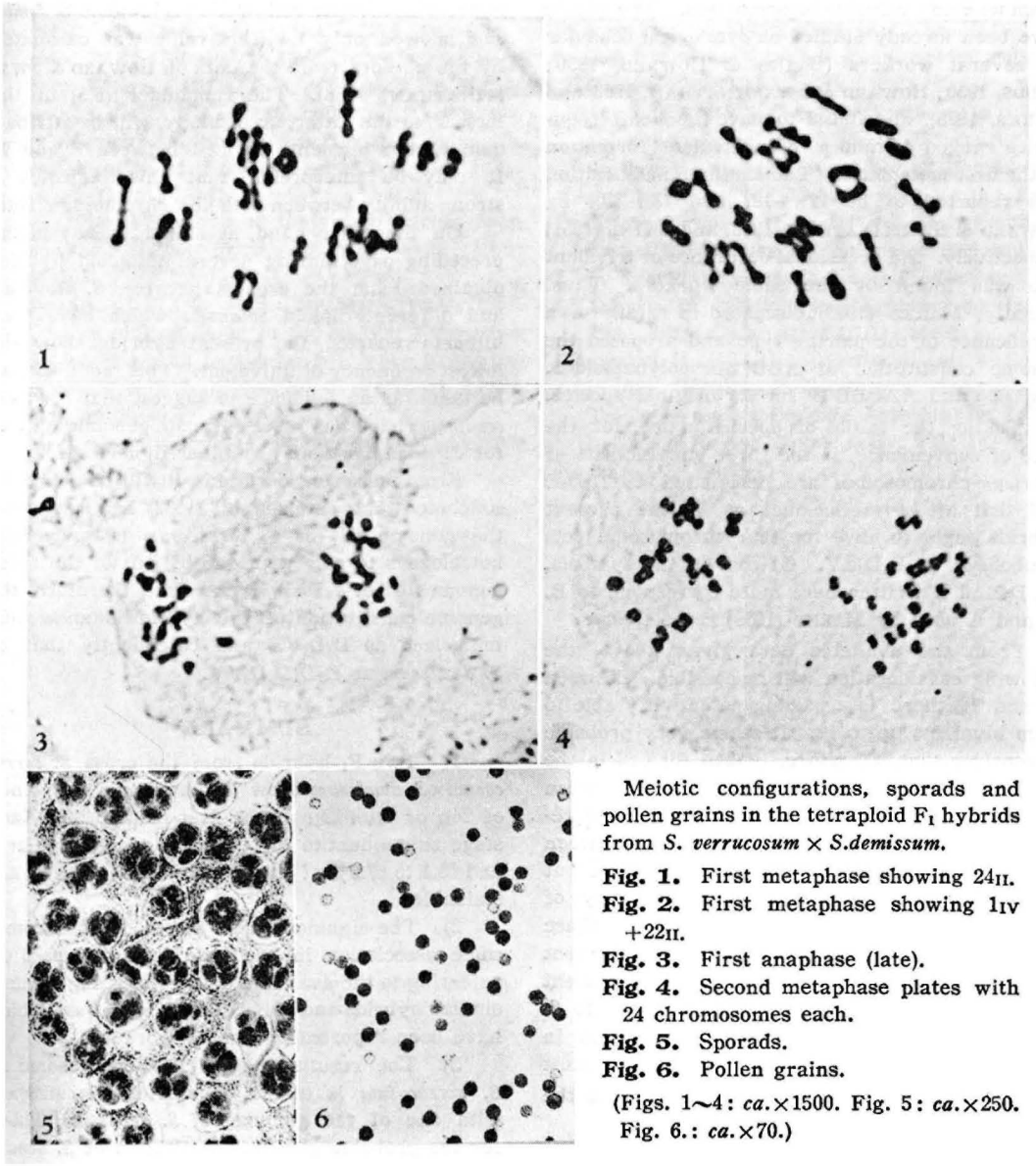
Table 4. Frequency of laggards at A-I and T-I in the hybrids.

	Number per cell 0	1	2	Total
Freq.	43	12	5	60
%	71.7	20.0	8.3	

Table 5. Chromosome uumber at M-II in the hybrids.

	Number per plate 22	23	24	25	26	Total
Freq.	3	32	68	16	1	120
%	2.5	26.7	56.7	13.3	0.8	

to about 37% of total number per cell of the bivalents (Table 3). Besides, one heteromorphic bivalent and two larger ones with rod form were found usually. Both the ranges of trivalents and quadrivalents were 0 to 2 and their mean frequencies were lower than in PROPACH's data (1937). All the quadrivalents observed were of 0-shape, except for some of N- and U-shaped ones. Each stage subsequent to the first metaphase proceeded nearly normally as will be mentioned below. At the first anaphase and telophase, the cells having no lagging chromosomes were counted in 71.7% of the cells examined and even if there were ones having them, they only showed at most one or two lagging or dividing univalents (Table 4 and Fig. 3). The chromosome distribution at the second metaphase are given in Table 5. The chromosome numbers per plate showed comparatively limited variation having a range of 22 to 26, the mode being at 24. In the hybrids 56.7%



Meiotic configurations, sporads and pollen grains in the tetraploid F_1 hybrids from *S. verrucosum* × *S.demissum*.

Fig. 1. First metaphase showing 24_{II}.
Fig. 2. First metaphase showing $1_{IV}+22_{II}$.
Fig. 3. First anaphase (late).
Fig. 4. Second metaphase plates with 24 chromosomes each.
Fig. 5. Sporads.
Fig. 6. Pollen grains.
(Figs. 1~4: *ca.*×1500. Fig. 5: *ca.*×250. Fig. 6.: *ca.*×70.)

of the second metaphase plates were of numerically balanced ones with 24 chromosomes. Fig. 4 shows the second metaphase plates with 24 chromosomes each. This value is by far higher than that of PROPACH (1937) who has calculated only 11% in similar hybrid.

At the sporad stage, 520 cells examined were sorted into 2 dyads, 2 triads, 505 tetrads, 9 pentads and 2 hexads. All the tetrads amounting to 97.1% of the sporads appeared normal, with four uniform microspores (Fig. 5). Pollen samples collected from two different plants in the hybrids were examined, and one plant was found to have 63.1% of stainable pollen grains and the other 67.0% (Fig. 6).

DISCUSSION

As mentioned above, pairing behavior of the hybrids used in the present work is shown by a mean frequency of $0.81_{IV}+0.42_{III}+21.32_{II}+0.89_{I}$. Since the maximum frequency, however, is 24_{II} or $1_{IV}+22_{II}$, a mode of chromosome association in the hybrids will be discussed mainly focusing on this type of pairing.

For that, prior to that, genome constitution of *S. demissum* with 36 chromosomes in the gametic number must be considered. In this respect, the studies on polyhaploid plants of this species have

given us many valuable informations. The plants have been already studied on cytological behavior by several workers (BAINS & HOWARD, 1950; DODDS, 1950; HOWARD & SWAMINATHAN, 1953 and MARKS, 1955). and found to have the mean frequencies ranged 4.7 and 9.78 in bivalent formation at the first metaphase. The maximum association was reported to be $12_{II}+12_{I}$ and $13_{II}+10_{I}$ by HOWARD & SWAMINATHAN (1953) and BAINS (1951) respectively. An occasional occurence of trivalent also was found by the same workers. Thus, recently, MARKS (1955) discussed in detail on a significance of the pairing type and proposed the genome constitution of ABB^{1} for polyhaploid *S. demissum* and AABBB^{1}B^{1} for its original species.

Taking the initial of species name, for the sake of convenience, if the three gametic sets of *demissum*-chromosomes are designated as D_1D_2E and that of *verrucosum*-ones as V, the present hybrids ought to have the four chromosome sets symbolized as D_1D_2EV. Of course, the symbols, D_1, D_2 and E written here quite correspond to B, B^{1} and A used by MARKS (1955) respectively.

From the available data given above, the following consideration will be possible. Between D_1 and D_2 there is a pairing potentiality able to form bivalents up to 12. It seems very probable to consider that, therefore, of 24_{II} formed in the hybrids, 12_{II} are made by autosyndesis between D_1 and D_2 and, as a consequence of this, the remaining 12_{II} may be derived from pairing between E and V. Supposing V did not mate with E but with either D_1 or D_2, a higher frequency of trivalent should be counted at the first metaphase than what will be found actually in the present materials. Whereas, there was a mean trivalent frequency of 0.4, showing a range of 0 to 2. This value is significantly too low to be in accordance with the supposition. Thus, a most probable mode of chromosome association in the hybrids may be schematized as follows:

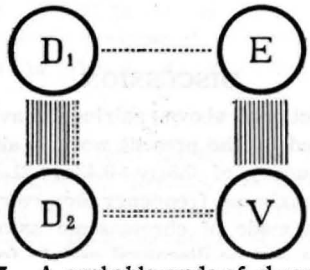


Fig. 7. A probable mode of chromosome association in the hybrids.

Furthermore, in the number of the ring bivalents closely paired with two chiasmata the hybrids had 7.9 per cell, while polyhaploid *S. demissum* showed only 1.4 (this value was calculated by the authors from the data of HOWARD & SWAMINATHAN, 1953). The remainder (6.5) of the former to the latter, accordingly, will be attributable to the bivalents formed between E and V. It may be interpreted that this indicates a strong affinity between both the chromosome sets.

On the other hand, as stated already in the preceding page, among several tetaploid hybrids obtained from the crosses between *S. demissum* and different diploid *Solanums* which have been hitherto reported, the present hybrids show the lowest frequency of univalent. This fact also may be taken as an evidence to suggest that *S. verrucosum* perhaps has more intimate genomic affinity for *S. demissum* than any other diploid species.

From these considerations, it will be able to be concluded that, as PROPACH (1937) has suggested, the genome (V) of *S. verrucosum* is sufficiently homologous to pair with one (E) out of the three genomes of *S. demissum*, and that, therefore, the genome constitution of the hybrid is anew formularized as D_1D_2VV and cosequently that of *S. demissum* as $D_1D_1D_2D_2VV$.

SUMMARY

1) Two F_1 hybrids from the cross *S. verrucosum*×*S. demissum* show the maximum frequency of 24_{II} or $1_{IV}+22_{II}$ at the first metaphase. Each stage subsequent to this proceeds nearly regularly and 63.1 to 67.0% of the pollen grains counted are stainable.

2) The significance of the mode of chromosome association in the hybrids is discussed on referring to the available data concerning several similar hybrids and polyhaploid *S. demissum*, which have been reported by earlier workers.

3) The results suggest that the genome of *S. verrucosum* is almost completely homologous with one of the genomes of *S. demissum*. Thus, for the probable genome constitution of *S. demissum*, $D_1D_1D_2D_2VV$ is proposed.

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