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Matsubayashi, Motokazu

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

XII. Intra- and Inter-Series Genomic Relationships in Diploid *Commersoniana* and *Tuberosa* Species

Motokazu MATSUBAYASHI*

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Abstract

Genomic relationships in diploid species within each of the two series ***Commersoniana*** (*COM*) and ***Tuberosa*** (*TUB*) and between both were assessed by measuring crossability between the diploid species and by observing meiotic behaviors of the diploid hybrids and their tetraploid derivatives. The results obtained are summarized in the following.

1) The *COM* diploid species, except *S.* ***commersonii*** (***cmm***), were highly crossable with one another. All the diploid hybrids, apart from the ones involving ***cmm***, had regular meiotic pairing, 12_{I}, in more than 96% of the cells at metaphase I, and showed considerably regular chromosome behaviors at subsequent stages to give pollen and seed fertilities as high as their parents. In the hybrids obtained using ***cmm***, however, there was found the occasional occurrence of a tetrapartite association at diakinesis and also of laggards and chromatid bridges at anaphase I. Their fertilities were fairly reduced both in pollen and seed. All the amphidiploids from the diploid hybrids had higher multivalent frequencies than in their parental autotetraploids, except the one involving ***cmm*** which had significantly lower frequency.

2) The *TUB* diploid species also were crossed readily with one another. All the diploid hybrids showed 12_{I} in about 90% of the cells and were regular in subsequent behaviors. They were 70～80% pollen stainable, except the dihaploid *S.* ***tuberosum*** × *S.* ***rybinii*** hybrid which had only 27.6%. The amphidiploids, with a few exceptions, formed multivalents at higher frequency than in their parental autotetraploids.

3) Inter-series crosses in the above two series succeeded readily, though showing a lower crossability than in the intra-series crosses. The diploid hybrids had 12_{I} in about 80% of the cells at metaphase I, but differed from the intra-series ones in possessing occasional heteromorphic bivalents and also in showing slightly higher frequencies of such irregularities as observed especially in the ***cmm*** hybrids at subsequent stages. Their fertilities were somewhat lower than those in the intra-series hybrids. In the amphidiploids there was found the multivalent formation at significantly high frequency as compared with their parental autotetraploids.

4) From the results obtained, it may be concluded as follows : the *COM* diploid species have highly homologous genomes, but the ***cmm*** genome is somewhat differentiated from them, although basically similar ; the *TUB* diploid species also have highly homologous genomes ; the diploid species of both series are closely related in possessing quite similar genomes ; and the genome symbol AA is thus assigned to all of these species.

Introduction

The section *Petota* (formerly *Tuberarium*) of the genus *Solanum* has recently been classified into 18 taxonomic series by HAWKES5). Of these series, the series *Commersoniana* comprises the species which are native to Argentina and its

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* Laboratory of Plant Breeding

neighboring countries and possess genes for insect resistance, and the series *Tuberosa* consists of the species which are distributed all over the Andean highlands, concentrating in Peru and Bolivia, several of which being cultivated types [3,5].

A number of species hybrids between the two series as well as within each of them have so far been studied cytogenetically by many workers[1,2,8-10,12,13,19,20,22]. However, our knowledge of intra- and inter-series genome relationships is as yet somewhat less satisfactory, though a useful information in this rerpect has appeared from Swaminathan's work[20].

The present study, thus, was undertaken to approach to a satisfactory solution of this problem, using some diploid species belonging to the series in question. This paper reports the results obtained by examining, from such a point of view, crossability between the species concerned, meiotic behavior and fertility in diploid hybrids, and multivalent frequency in amphidiploids and their parental autotetraploids.

Materials and Methods

The materials used in the present study comprise diploid F_1 hybrids obtained using the diploid *Solanum* species (2n=24) listed in Table 1 and their tetraploid derivatives.

Of the species described in the table, *chc* had been supplied from the Max-Planck-Institut für Züchtungsforschung, Köln-Vogelsang, and the others, except *spl* and *tbr*-2x, had been supplied from the Inter-regional Potato Introduction Station, Wisconsin. *Spl* is one of the *Solanum* materials collected by the present author at Cochabamba in Bolivia, and *tbr*-2x is one of dihaploid clones (2n=24) detected from among *tbr* × *phu* hybrid progenies. Tetraploid materials were all induced from the diploid hybrids and their parental species by tuber treatment with colchicine employing the method described elsewhere[7]. The materials were potted and grown in a glasshouse during all the growing period from February to June.

Interspecific crosses were reciprocally attempted within and between the two taxonomic serise, *COM* and *TUB*, under glasshouse conditions. For each of the successful crosses, measurements were made on the berry setting percentage, the number of seeds per berry and the seed germination percentage, and crossability was estimated by multiplying together these measurements, the value thus obtatned being equivalent to the P.P.P. value proposed by Marks[11]. Meiotic configurations were analyzed in P.M.C. squashes prepared employing the acetocarmine technique modified by the present author[14]. Pollen preparations were made by staining with a dilute acetocarmine solution and the percentage of

Table 1. Diploid *Solanum* species studied

Species[1]	Taxonomic[2] series	Sources
S. chacoense (*chc*)	*Commersoniana* (*COM*)	Nr. R49/58
S. commersonii (*cmm*)	,,	PI 197760
S. saltense (*slt*)	,,	PI 189217
S. schickii (*sch*)	,,	PI 189218
S. phureja (*phu*)	*Tuberosa* (*TUB*)	PI 225667
S. rybinii (*ryb*)	,,	PI 197761
S. sparsipilum (*spl*)	,,	Collected in Bolivia
S. stenotomum (*stn*)	,,	PI 195204×205526
S. vernei (*vrn*)	,,	PI 230468
Dihaploid *S. tuberosum* (*tbr*-2x) cv. Deodara	,,	Induced by the present author

1) and 2) The letters parenthesized are based on the three letter code system proposed by Simmonds (1963) for series and species names. *Slt* and *sch* have been included in *chc* and *ryb* in *phu* by Hawkes (1963).

normal-shaped and well stained grains was used as a criterion for assessing pollen fertility. Seed fertility was measured by the mean number of seeds per pollination.

Results

Crossability between Diploid Species

Diploid interspecific crosses were reciprocally made within and between the two series, *COM* and *TUB*, and the results are given in Table 2. As seen from this table, all of the *COM* species used, except *cmm*, were quite readily crossed with one another, giving high crossability values amounting to 90 or more. Comparing with the above, the crosses using *cmm* were fairly difficult, especially when this species was used as the male parent, the crossability values being only between 2.3 and 18.2. In the interspecific crosses within the series *TUB*, crossability was found to be markedly high in *stn*×*ryb* and *phu* ×*stn*, moderately high in *stn*×*spl*, and comparatively low in the other combinations, its value being 50 or less. Particularly, the crosses between *tbr*-2x and *ryb* produced only 1~2 seeds per pollination in both directions.

On the other hand, the crosses between the series *COM* and *TUB* were somewhat difficult as compared with the above intra-series crosses. The crossability found here was comparatively low in all combinations, except the cross *chc*× *spl* which gave 135.8 in its value, and was markedly reduced when the *TUB* species were used as female parents. *Tbr*-2x was successful with difficulty only as females in crosses with the *COM* species, yielding a very few seeds per pollination.

Meiotic Behavior of Diploid Hybrids

Intra-series hybrids

In Tabel 3 are summarized the results ob-

Table 2. Results of interspecific crosses in *COM* and *TUB* species

Cross combination	No. of flowers polli.	Berry setting		No. of seeds/berry		Seed germinability (%)	Cross-ability 1)
		No.	%	Mean	Range		
Intra-series(*COM*)							
chc × *slt*	25	22	88.0	184.6	86~260	98.0	159.2
Reciprocal	20	19	95.0	154.3	81~245	96.0	140.7
chc × *sch*	20	16	80.0	159.0	66~196	73.3	93.2
Reciprocal	20	16	80.0	122.5	102~146	97.5	95.6
cmm × *chc*	22	14	63.6	116.4	70~157	86.3	63.9
Reciprocal	27	3	11.1	28.3	22~ 35	83.3	2.6
cmm × *slt*	20	14	70.0	88.7	45~125	80.0	49.7
Reciprocal	27	3	11.1	33.5	26~ 41	61.5	2.3
cmm × *sch*	21	20	95.2	131.8	36~260	70.4	88.3
Reciprocal	26	13	50.0	51.3	17~ 83	70.8	18.2
sch × *slt*	20	20	100.0	185.0	156~214	93.5	173.0
Reciprocal	20	19	95.0	232.8	60~293	95.0	210.1
Intra-series(*TUB*)							
ryb × *stn*	41	25	61.0	66.4	17~126	81.0	32.8
Reciprocal	24	20	83.3	178.1	85~340	87.1	129.2
phu × *stn*	18	14	77.8	311.6	27~535	55.0	133.3
Reciprocal	20	8	40.0	167.0	6~624	53.1	35.5
ryb × *spl*	24	12	50.0	120.8	19~318	87.5	52.9
Reciprocal	18	4	22.2	103.5	100~107	90.0	20.7
stn × *spl*	99	58	58.6	261.8	12~365	57.1	87.6
Reciprocal	79	26	32.9	104.0	34~255	97.3	33.3
tbr-2x × *ryb*	20	4	20.0	1.5	1~2	84.0	0.3
Reciprocal	36	0	0	0	0	0	0

Inter-series(*COM-TUB*)							
chc × ***ryb***	21	12	57.1	135.6	68~254	75.7	58.6
Reciprocal	18	12	66.7	40.1	11~ 64	84.8	22.7
chc × ***spl***	14	10	71.4	219.4	120~259	86.7	135.8
cmm × ***ryb***	20	12	60.0	69.1	21~103	75.0	31.1
Reciprocal	20	10	50.0	87.8	55~120	76.7	33.9
slt × ***ryb***	21	20	95.2	93.3	42~132	84.0	74.6
Reciprocal	20	8	45.0	48.3	15~ 74	76.7	16.6
sch × ***ryb***	20	15	75.0	102.9	38~148	90.0	69.5
Reciprocal	22	20	90.9	121.6	46~194	90.0	99.5
sch × ***stn***	28	18	64.3	153.0	115~196	75.0	73.8
Reciprocal	24	10	41.7	55.2	36~ 98	70.0	16.1
slt × ***stn***	28	13	46.4	47.2	15~ 68	60.0	13.1
Reciprocal	20	10	50.0	97.3	25~202	60.8	29.6
tbr-2x × ***chc***	24	9	37.5	4.6	3~8	25.0	0.4
Reciprocal	25	0	0	0	0	0	0
tbr-2x × ***cmm***	18	3	16.7	1.3	1~2	0	0
Reciprocal	23	0	0	0	0	0	0
tbr-2x × ***sch***	20	8	40.0	6.3	4~11	33.3	0.8
tbr-2x × ***slt***	22	2	9.1	2.0	1~3	0	0

1) For explanation, see text.

Table 3. Meiotic pairing in intra-series diploid hybrids

Hybrids	Meiotic stage	No. of cells observ.	Mean (+S.E.) & range (*Italic*) in number per cell			
			IV	III	II	I
COM						
F$_1$, *slt*×*chc*	Diak.	30			12.00±0.00 *(12)*	
	M-I	115			11.97±0.02 *(11~12)*	0.05±0.03 *(0~2)*
F$_1$, *chc*×*sch*	Diak.	36			12.00±0.00 *(12)*	
	M-I	65			12.00±0.00 *(12)*	
Reciprocal	Diak.	30			12.00±0.00 *(12)*	
	M-I	84			11.98±0.02 *(11~12)*	0.05±0.03 *(0~2)*
F$_1$, *cmm*×*chc*	Diak.	50	0.02±0.02 *(0~1)*		11.90±0.04 *(10~12)*	0.09±0.07 *(0~2)*
	M-I	62			11.60±0.08 *(10~12)*	0.81±0.16 *(0~4)*
Reciprocal	Diak.	45	0.02±0.02 *(0~1)*		11.91±0.05 *(10~12)*	0.09±0.06 *(0~2)*
	M-I	58			11.72±0.07 *(10~12)*	0.55±0.15 *(0~4)*
F$_1$, *cmm*×*slt*	Diak.	42			11.81±0.07 *(10~12)*	0.38±0.14 *(0~4)*
	M-I	68			11.65±0.07 *(10~12)*	0.71±0.15 *(0~4)*
Reciprocal	Diak.	38	0.03±0.03 *(0~1)*		11.82±0.07 *(10~12)*	0.26±0.11 *(0~2)*
	M-I	62			11.76±0.07 *(10~12)*	0.48±0.14 *(0~4)*

F₁, *cmm*×*sch*	Diak.	34	11.88±0.06 (*11~12*)	0.24±0.11 (*0~2*)
	M-I	70	11.68±0.07 (*10~12*)	0.63±0.13 (*0~4*)
F₁, *sch*×*slt*	Diak.	40	12.00±0.00 (*12*)	
	M-I	56	11.96±0.03 (*11~12*)	0.07±0.05 (*0~2*)
TUB				
F₁, *ryb*×*stn*	Diak.	45	12.00±0.00 (*12*)	
	M-I	100	11.98±0.01 (*11~12*)	0.04±0.03 (*0~2*)
Reciprocal	Diak.	22	12.00±0.00 (*12*)	
	M-I	83	11.94±0.03 (*11~12*)	0.12±0.05 (*0~2*)
F₁, *phu*×*stn* Clone 1	Diak.	32	12.00±0.00 (*12*)	
	M-I	50	11.96±0.03 (*11~12*)	0.08±0.06 (*0~2*)
Clone 2	Diak.	29	12.00±0.00 (*12*)	
	M-I	60	11.98±0.02 (*11~12*)	0.03±0.03 (*0~2*)
Reciprocal Clone 1	Diak.	37	11.97±0.03 (*11~12*)	0.05±0.05 (*0~2*)
	M-I	58	11.95±0.03 (*11~12*)	0.10±0.06 (*0~2*)
Clone 2	Diak.	34	12.00±0.00 (*12*)	
	M-I	53	11.98±0.02 (*11~12*)	0.04±0.04 (*0~2*)
F₁, *ryb*×*spl* Clone 1	Diak.	25	12.00±0.00 (*12*)	
	M-I	46	11.91±0.04 (*11~12*)	0.17±0.08 (*0~2*)
Clone 2	Diak.	30	11.93±0.05 (*11~12*)	0.13±0.09 (*0~2*)
	M-I	43	11.77±0.09 (*10~12*)	0.47±0.17 (*0~4*)
Clone 3	Diak.	31	11.97±0.03 (*11~12*)	0.06±0.06 (*0~2*)
	M-I	62	11.94±0.03 (*11~12*)	0.13±0.06 (*0~2*)
F₁, *vrn*×*ryb*	Diak.	31	11.94±0.04 (*11~12*)	0.13±0.09 (*0~2*)
	M-I	54	11.85±0.06 (*10~12*)	0.03±0.12 (*0~4*)
Reciprocal	Diak.	30	11.97±0.03 (*11~12*)	0.07±0.07 (*0~2*)
	M-I	52	11.92±0.04 (*11~12*)	0.15±0.07 (*0~2*)
F₁, *tbr*-2x×*ryb*	Diak.	52	11.96±0.03 (*11~12*)	0.08±0.05 (*0~2*)
	M-I	72	11.92±0.03 (*11~12*)	0.17±0.07 (*0~2*)

Table 4. Meiotic pairing in inter-series diploid hybrids

Hybrids	Meiotic stage	No. of cells observ.	Mean(+S. E.) & range (*Italic*) in number per cell II	I
COM-TUB				
F₁, *chc*×*ryb*	Diak.	45	11.89±0.05 (*11~12*)	0.22±0.09 (*0~2*)
	M- I	115	11.63±0.05 (*10~12*)	0.75±0.12 (*0~4*)
Reciprocal	Diak.	48	11.94±0.04 (*11~12*)	0.13±0.07 (*0~2*)
	M- I	80	11.88±0.04 (*11~12*)	0.25±0.07 (*0~2*)
F₁, *chc*×*spl* Clone 1	Diak.	36	12.00~0.00 (*12*)	
	M- I	48	12.00±0.00 (*12*)	
Clone 2	Diak.	30	12.00±0.00 (*12*)	
	M- I	50	11.96±0.03 (*11~12*)	0.08±0.06 (*0~2*)
F₁, *ryb*×*cmm*	Diak.	39	12.00±0.00 (*12*)	
	M- I	96	11.88±0.03 (*11~12*)	0.25±0.07 (*0~2*)
F₁ ,*slt*×*ryb*	Diak.	34	11.88±0.06 (*11~12*)	0.24±0.11 (*0~2*)
	M- I	92	11.76±0.05 (*10~12*)	0.48±0.10 (*0~4*)
Reciprocal	Diak.	30	11.90±0.31 (*11~12*)	0.20±0.11 (*0~2*)
	M- I	102	11.77±0.05 (*10~12*)	0.47±0.09 (*0~4*)
F₁, *sch*×*ryb*	Diak.	22	11.91±0.06 (*11~12*)	0.18±0.13 (*0~2*)
	M- I	82	11.88±0.04 (*10~12*)	0.24±0.08 (*0~4*)
Reciprocal	Diak.	35	11.97±0.03 (*11~12*)	0.06±0.06 (*0~2*)
	M- I	55	11.91±0.04 (*11~12*)	0.18±0.08 (*0~2*)
F₁, *sch*×*stn*	Diak.	30	11.97±0.03 (*11~12*)	0.07±0.07 (*0~2*)
	M- I	100	11.84±0.05 (*11~12*)	0.32±0.11 (*0~2*)
F₁, *stn*×*slt*	Diak.	36	11.94±0.04 (*11~12*)	0.11±0.08 (*0~2*)
	M- I	50	11.82±0.06 (*10~12*)	0.36±0.12 (*0~4*)
F₁, *tbr*-2x×*chc* Clone 1	Diak.	45	12.00±0.00 (*12*)	
	M- I	162	11.96±0.02 (*11~12*)	0.09±0.03 (*0~2*)
Clone 2	Diak.	52	11.87±0.05 (*11~12*)	0.27±0.09 (*0~2*)
	M- I	215	11.78±0.03 (*10~12*)	0.44±0.06 (*0~4*)

tained by analyzing pairing behaviors at diakinesis and metaphase I in diploid hybrids within each of the series *COM* and *TUB*.

In the series *COM*, all the hybrids, apart from the ones obtained using *cmm*, showed regular pairing, 12_{II}, in 96% or more of the cells observed. Most of the bivalents were of rod-shape with a single chiasma and ring bivalents joined by two chiasmata were found at frequencies ranging 2 to 4 per cell. Univalents were rarely present and their occurrence was not due possibly to the failure of pairing but to precocious separation (Fig. 1 c). Similar meiotic configurations have also been described by earlier workers [9,12,20] for certain diploid hybrids in the same series. Hybrids involving *cmm*, however, differed to some extent from the above ones in having occasionally a tetrapartite association as shown in Fig. 1a and univalents at a higher frequency (0.48~0.81 per cell). Such a tetrapartite association seems to be due to translocation heterozygosity in some chromosomes of these hybrids.

At anaphase I, chromosome separation occurred regularly in all the hybrids. The hybrids involving *cmm*, however, had laggards and chromatid bridges in 21.4~25.2% and 0.17~0.30% of the cells, respectively, while these configurations were of rare or no occurrence in the other hybrids. At metaphase II, chromosome distribution was usually normal in all instances, with the exception of the hybrids involving *cmm* in which there were present scattered chromosomes with a fairly high frequency, *i. e.* 1 ~ 3 per cell in 17.7 ~ 20.8 %

of the cells examined. Balanced plates with 12 chromosomes as well as normal tetrads occurred less frequently in the preceding *cmm* hybrids than in the other hybrids.

A quite similar pattern of meiotic pairing was also encountered at diakinesis and metaphase I in the diploid hybrids within the series *TUB*, though there was found a slight reduction in bivalent frequency. All the hybrids concerned had 12_{II} in 90% or more of the cells observed. Ring bivalents were present with a somewhat higher frequency than in the *COM* hybrids, ranging from 2 to 6 per cell, with a mean of 4.

Meiosis of the *TUB* diploid hybrids has so far been observed by many workers[1,2,8,12,13,20,22], since Rybin[19] first studied it, and the results given by them are in close agreement with those in the preseent study. Chromosome behaviors at anaphase I and metaphase II were usually regular in all of the hybrids, except for *tbr*-2x ×*ryb* hybrids. In the last-mentioned hybrids, there were found a few laggards and chromatid bridges at anaphase I in 8.7% and 0.49% of the cells examined, respectively, whereas these irregularities were hardly encountered in the other hybrids. Balanced plates at metaphase II were

Table 5. Fertility of intra- and inter-series hybrids

Hybrids	Pollen fertility			Seed fertility	
	Pollen stainability (%)	Index 1)	2n pollen (%)	Mean no. of seeds per polli.	Index 2)
Intra-series hybrids(*COM*)					
F_1, *slt*×*chc*	94.3	111.9	0	129.6	182.8
F_1, *chc*×*sch*	92.1	110.7	0.08	105.0	121.9
Reciprocal	97.8	117.5	0.07	115.9	134.6
F_1, *cmm*×*chc*	72.3	75.6	0.08	22.6	24.3
Reciprocal	78.2	81.8	0	13.2	14.2
F_1, *cmm*×*slt*	70.8	73.4	0.01	26.3	25.7
Reciprocal	75.6	78.3	0	12.2	11.9
F_1, *cmm*×*sch*	70.1	85.0	0.03	52.2	42.8
F_1, *sch*×*slt*	91.5	108.5	0	107.5	113.2
Intra-series hybrids(*TUB*)					
F_1, *ryb*×*stn*	70.6	72.2	0.19	23.4	28.0
Reciprocal	77.7	76.8	0.06	33.1	39.5
F_1, *phu*×*stn*	79.5	113.2	0.40	33.4	58.6
Reciprocal	78.9	112.4	0.11	42.9	75.3
F_1, *ryb*×*spl*	85.6	114.7	0.09	23.6	37.7
F_1, *vrn*×*ryb*	72.4	104.8	—	—	—
F_1, *vrn*×*stn*	70.8	95.9	—	—	—
F_1, *tbr*-2x×*ryb*	27.6	81.4	16.12	13.6	14.1
Inter-series hybrids(*COM*-*TUB*)					
F_1, *chc*×*ryb*	88.4	113.9	0.02	68.1	78.6
Reciprocal	77.8	100.3	0.24	25.2	29.1
F_1, *chc*×*spl*	90.5	97.4	0	17.8	26.6
F_1, *ryb*×*cmm*	70.6	92.7	0.02	29.7	28.4
F_1, *slt*×*ryb*	74.0	93.9	0	26.4	28.9
Reciprocal	74.1	94.0	0.08	26.9	29.4
F_1, *sch*×*ryb*	78.6	117.0	0	80.8	80.2
Reciprocal	77.1	114.7	0	22.1	21.9
F_1, *sch*×*stn*	76.5	108.2	0	36.6	45.2
F_1, *stn*×*slt*	68.4	79.0	0.29	18.4	22.7
F_1, *tbr*-2x×*chc* Clone 1	70.3	148.9	4.79	7.6	11.9
Clone 2	0	—	—	10.8	16.9

1) and 2) For explanation, see text.

Table 6. Comparisons of amphidiploids with their parental autotetraploids for multivalent frequency

Material	No. of cells observ.	Percentage frequency of cells with multivalents of										Mean freq. per cell (±S.E.)	Multi-valent coefficient[1]	L. S. D.[2]	
		0	1	2	3	4	5	6	7	8	9			Female	Male
Amphidiploids															
Intra-series(*COM*)															
cmm×*chc*	46	0	2.2	2.2	**39.1**	30.4	26.1	0	0	0	0	3.76±0.14	29.26	** −	
sch×*chc*	48	0	0	4.2	12.5	**41.7**	37.5	4.2	0	0	0	4.25±0.13	33.33	** +	
chc×*sch*	50	0	0	4.0	12.0	**40.0**	32.0	12.0	0	0	0	4.36±0.14	34.67		** +
slt×*chc*	47	0	0	4.3	19.1	**27.7**	**27.7**	17.0	4.3	0	0	4.47±0.18	35.51		** +
Intra-series(*TUB*)															
vrn×*ryb*	59	0	8.5	18.6	**28.8**	25.4	16.9	1.7	0	0	0	3.29±0.16	26.77	** −	* −
vrn×*stn*	60	0	3.3	13.3	**30.0**	26.7	23.3	3.3	0	0	0	3.63±0.15	29.20	** −	
phu×*stn* Cl. 1	51	0	0	5.9	15.7	**33.3**	23.5	17.6	2.0	2.0	0	4.45±0.18	36.19		
,, Cl. 2	52	0	1.9	0	15.4	**38.5**	25.0	11.5	1.9	5.8	0	4.56±0.19	37.62		* +
stn×*ryb*	65	0	0	3.1	9.2	18.5	27.7	**29.2**	4.6	4.6	3.1	5.18±0.18	42.37	** +	** +
ryb×*stn*	60	0	0	1.7	6.7	13.3	26.7	**30.0**	16.7	5.0	0	5.47±0.17	44.44	** +	** +
ryb×*spl* Cl. 1	50	0	0	2.0	10.0	6.0	20.0	**28.0**	16.0	12.0	6.0	5.88±0.24	46.38	** +	** +
,, Cl. 2	48	0	0	2.1	8.3	4.2	20.8	**33.3**	14.6	12.5	4.2	5.90±0.23	46.61	** +	** +
Inter-series(*COM*-*TUB*)															
stn×*slt*	62	8.1	25.8	**27.4**	25.8	12.9	0	0	0	0	0	2.10±0.15	16.70	** −	** −
ryb×*slt*	72	2.8	19.4	27.8	**36.1**	13.9	0	0	0	0	0	2.39±0.12	18.68	** −	** −
sch×*stn*	70	2.9	8.6	28.6	**40.0**	11.4	8.6	0	0	0	0	2.74±0.14	21.07	* −	** −
slt×*ryb*	72	0	2.8	**36.1**	33.3	27.8	0	0	0	0	0	2.86±0.10	22.40	** −	** −
chc×*ryb*	52	0	0	30.8	**34.6**	32.7	1.9	0	0	0	0	3.06±0.12	24.52	** −	** −
sch×*ryb*	52	0	0	19.2	**53.9**	23.1	3.8	0	0	0	0	3.12±0.11	25.08		** −
ryb×*sch*	62	0	0	16.1	**38.7**	35.5	9.7	0	0	0	0	3.34±0.11	27.42	** −	
chc×*spl*	57	0	3.5	17.5	**35.1**	19.3	15.8	7.0	1.8	0	0	3.54±0.18	28.44		* −
ryb×*cmm*	84	0	0	14.3	27.4	**28.6**	26.2	3.6	0	0	0	3.77±0.12	29.91		** −
Parental autotetraploids															
COM															
sch	90	0	5.5	21.1	**36.6**	16.7	13.3	6.7	0	0	0	3.31±0.14	25.93		
chc	72	0	2.1	11.1	20.8	**34.7**	25.0	4.2	1.4	0	0	3.87±0.14	31.16		
slt	53	0	0	5.7	11.3	**35.8**	32.1	15.1	0	0	0	4.39±0.15	35.14		
cmm	61	0	0	4.9	11.5	22.9	**45.9**	14.8	0	0	0	4.54±0.13	36.78		
TUB															
ryb	80	1.3	1.3	10.0	22.5	**37.5**	21.2	6.3	0	0	0	3.82±0.13	30.60		
spl	69	0	3.4	5.1	23.7	**39.0**	22.0	6.8	0	0	0	3.92±0.15	31.57		
stn	68	0	2.9	10.3	16.2	**35.3**	23.5	11.8	0	0	0	4.02±0.15	33.03		
phu	66	0	3.0	6.1	18.2	**34.8**	25.8	10.6	1.5	0	0	4.12±0.15	33.46		
vrn	60	0	1.7	6.7	13.3	**36.7**	23.3	18.3	0	0	0	4.28±0.16	34.72		

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1) For explanation, see text.

2) * and ** indicate significant difference from both the parental autotetraploids by L.S.D. at 5% and 1% levels of probability, respectively. + and − signify higher and lower multivalent frequencies than in the parental autotetraploids, respectively.

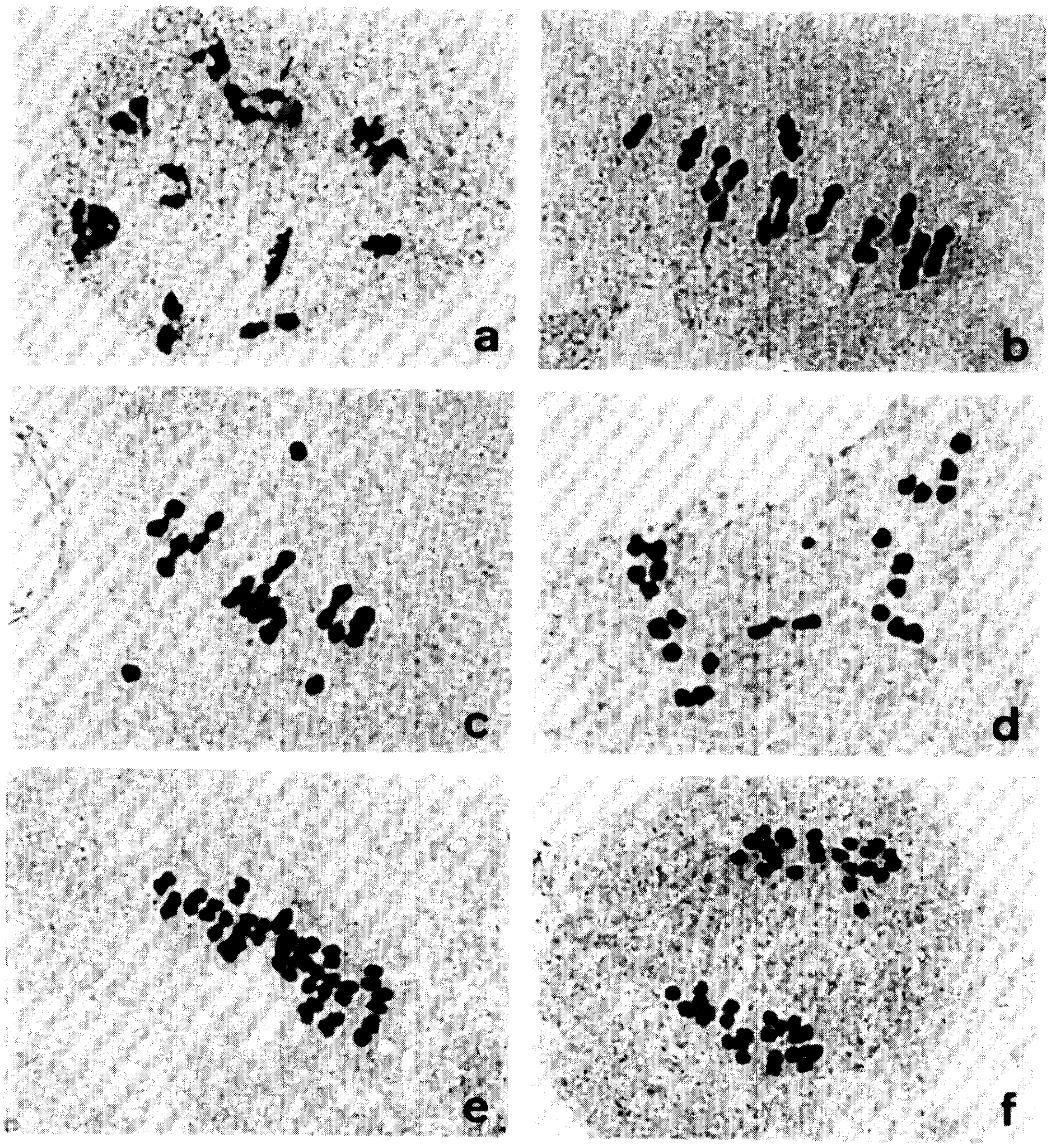

Fig. 1. Meiotic configurations in the diploid F_1 hybrids (*ca.*×1800).
a. Diakinesis in *cmm*×*chc*, $1_{IV} + 10_{\mathbf{I}}$, with a tetrapartite association (indicated by arrow) ; b. Metaphase I in *chc* × *ryb*, $12_{\mathbf{I}}$, with a few heteromorphic bivalents (indicated by arrows) ; c. Metaphase I in *slt* ×*cmm*, $11_{\mathbf{I}} + 2_{I}$, with 2 univalents which occurred due to precocious separation ; d. Anaphase I in *sch*×*stn*, showing a chromatid bridge resulting probably from translocation heterozygosity ; e. Metaphase II in *tbr*–2x×*chc*, with diploid number of dyad chromosomes arranged on equator ; f. Anaphase II in *tbr*–2x×*chc*, showing monad chromosome separation following the stage shown in Fig. 1e.

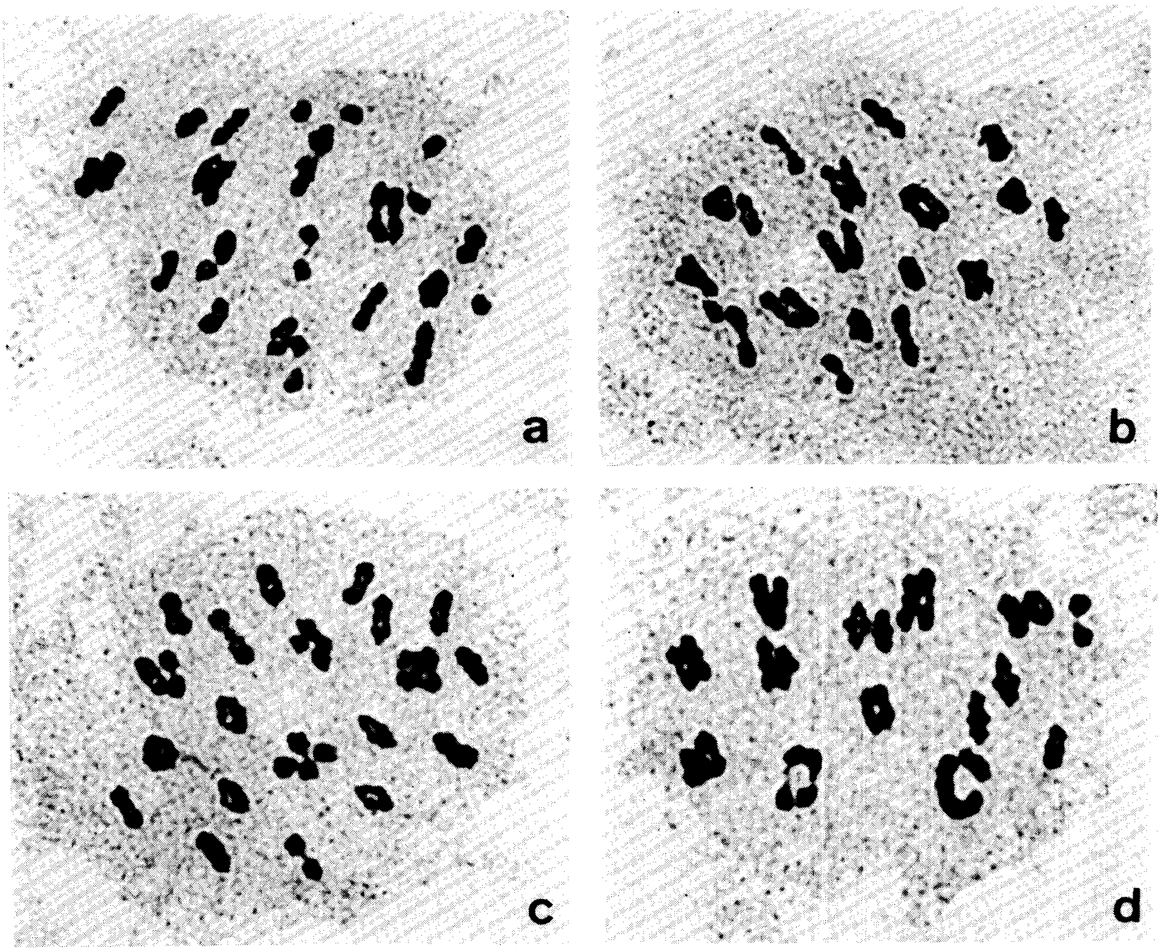

Fig. 2. Metaphase I configurations in the amphidiploids and their parental autotetraploids (*ca.*×1800).
a. *cmm*×*chc* amphidiploid, $3_{IV}+18_{I}$; b. *ryb*×*stn* amphidiploid, $5_{IV}+14_{I}$; c. *slt*×*stn* amphidiploid, $2_{IV}+20_{I}$; d. *vrn* autotetraploid, $6_{IV}+12_{I}$.

found with a lower frequency (91.1%) in the *tbr*-2x × *ryb* hybrids than in the others which had the frequencies of 96.5~98.5%. At sporad stage, normal tetrads occurred at the frequencies of 53.0~64.0% in the latter but only 30.7% in the former. Such a reduced frequency of normal tetrads in the *tbr*-2x × *ryb* hybrids seems to be ascribable to the frequent occurrence of the dyad formation resulting mostly from such abnormal division that diploid number of half bivalents is arranged on equator at the stage corresponding to metaphase II (Fig. 1 e & f).

Inter-series hybrids

For the *COM-TUB* diploid hybrids, their meiotic configurations were analyzed at diakinesis and metaphase I and the results are summarized in Table 4. All of the hybrids did usually show regular meiotic pairing at these stages. However, as compared with the above intra-series hybrids, there was found a reduced frequency of bivalents in these instances, showing 12_{I} in as much as 80% of the cells at metaphase I. Similar observations have also been made by some workers[8,12,13,20,22]. Multipartite configurations were not encountered at all in any instances. Unlike the intra-series hybrids, these hybrids had heteromorphic bivalents at the frequencies ranging 1 to 3 per cell, with a mean of 2 (Fig. 1 b). A few ring bivalents were present in every instances. Anaphase I separation and metaphase II distribution of chromosomes proceeded in comparatively regular manner in all the hybrids. In these instances, however, there occurred more frequently laggards and chromatid bridges at anaphase I and scattered chromosomes at metaphase II than in the intra-series hybrids. The chromatid bridges found here were accompanied by acentric fragments, suggesting that they may probably result from inversion heterozygosity (Fig. 1 d).

More than 85.1% of the sporads scored were normal tetrads. While the *tbr*-2x × *chc* hybrids were nearly similar to the other ones in meiotic behavior, the former differed from the latter in showing the frequent occurrence of abnormal division such as described above, leading to the formation of dyads in 5.8% of the sporads.

Fertility of Diploid Hybrids

Table 5 shows pollen and seed fertilities of the hybrids concerned, both with the observed values and their indices. In each case, the index was calculated as the ratio of the value observed in the hybrids to its bi-parental mean. Seed fertility was assessed by the mean number of seeds per pollination following sib-mating.

All the intra-series hybrids, with one exception, had high pollen fertility, the percentage of stainable pollen ranging 70.8 to 97.8% and their indices ranging 72.2 to 117.5. In this respect, these hybrids proved to be as fertile as their parental species themselves. The one exception was the hybrids involving *tbr*-2x which had 27.6 % stainable pollen. Also, the inter-series hybrids, except Clone 2 of the *tbr*-2x × *chc* ones, all were pollen fertile, showing pollen stainability above 70%. Unreduced or 2n pollen grains were detected in 17 out of the 28 hybrids used and their occurrence frequencies varied from 0.01 to 16.12%. Among these, the hybrids involving *tbr*-2x were marked to have such grains with the especially high frequencies amounting to 4.79~16.12%.

All the *COM* hybrids, except the ones involving *cmm*, as well as the hybrids from *stn* × *ryb*, *chc* × *ryb* and *sch* × *ryb* gave comparatively high seed fertility indices as high as 80, but the other hybrids showed considerably low values as presented in Table 5.

Multivalent Formation in Amphidiploids and Their Parental Autotetraploids

As has been done already in previous work [16,17], 'amphidiploid method' was employed for detecting cryptic structural differences of chromosomes between the perental genomes. In Table 6 is given a summary of the results obtained by this method. The multivalent coefficient presented in this table was calculated as percentage of the total number of chromosomes involved in the formation of multivalents (quadrivalents + trivalents).

Of the amphidiploids induced from the intra-series hybrids of the series *COM*, the one from *cmm* × *chc* had the significantly low frequency of multivalents as compared with their female parental autotetraploids, but the other ones were almost similar to or even higher than their parental autotetraploids in multivalent frequency. Similarly, the high multivalent frequencies were also encountered in the amphidiploids from the *TUB* diploid hybrids, except the *vrn*×*ryb* and *vrn*×*stn* amphidiploids, both having the significantly reduced multivalent frequencies. Fig. 2 a and b each show one of the metaphase I configurations observed in the intra-series amphidiploids in the series *COM* and *TUB*, respectively.

On the other hand, the inter-series amphidiploids were found to show a significant reduction in multivalent frequency in all instances as compared with one of their parental autotetraploids or with both (Fig. 2 c & d). In this respect, these amphidiploids were apparently distinguishable from the intra-series ones. Similar situation has also been reported by SWAMINATHAN and HOWARD[21] for amphidiploids from *stn*×*slt* and *chc*×*ryb*.

Discussion

Intra-Series Genome Relationships

As described in the preceding section, the hybrids between diploid species belonging to the series *COM*, except those involving *cmm*, all were highly regular in meiotic behavior and showed fertility as high as their parental species. In addition, the multivalent frequencies found in the amphidiploids induced from them were quite similar to or rather higher than those in their parental autotetraploids, indicating that random pairing of chromosomes occurred between the parental genomes. These facts suggest strongly, as pointed out already by some workers[3,6,12,13], that the genomes of the *COM* species not including *cmm* are highly homologous with one another. The hybrids involving *cmm* did somewhat differ from the above in having occasionally a tetrapartite configuration resulting probably from heterozygosity for a reciprocal translocation involving 4 chromosomes at diakinesis and in showing, as a result, more irregular behaviors of chromosomes at the later stages and a little reduction in fertility. Further, in the amphidiploids from these hybrids there was observed a significantly lower frequency of multivalents than in their parental autotetraploids. The genome of *cmm*, therefore, may be considered to comprise some chromosomes which differentiated slightly from those of the genomes of the other *COM* species. This will also be substantiated from the obviously reduced crossability in crosses using *cmm* as either parent. From this view, it seems to be reasonable that HAWKES[3,4,5] has treated *cmm* as a distinct species in the series *COM*.

The diploid hybrids in the series *TUB*, with a few exceptions, were observed to behave in entirely similar manner during their meiotic course to the *COM* diploid hybrids mentioned above. Fertility of these hybrids was not so different from that of their parental species. The amphidiploids concerned were found to show the multivalent formation in rather higher frequency than their parental autotetrapoids. The *TUB* species used, thus, may be considered to possess in common a highly homologous genome.

Inter-Series Genome Relationships

The diploid hybrids between the *COM* and *TUB* were observed to have considerably regular meiosis and moderately high fertility, in agreement with the observations by earlier workers [8,12,13,20,22]. However, they were to some extent different from the above intra-series hybrids in showing somewhat higher frequencies of such meiotic irregularities as univalents at metaphase I, laggards and chromatid bridges at anaphase I and scattered chromosomes at metaphase II. In addition, unlike the intra-series amphidiploids, the inter-series ones were found to form multivalents with significantly low frequencies as compared with their parental autotetraploids, indicating that some of the chromosomes of parental genomes tend to pair preferentially with their identical partners. This, in turn, will be taken as evidence to suggest the existence of chromosome structural differences, though of cryptic nature, between the parental genomes. Nevertheless, the multivalent frequency scored in the amphidiploids as well as the meiotic regularity and fertility found in the diploid hybrids seem to be too high to judge the parental genomes as being disimilar to each other. In tuberous *Solanums*, as a rule, a criterion for deciding certain two genomes as disimilar or non-homologous, the present author thinks, should be set up only in the case that such meiotic features as observed by Ramanna and Hermsen [18] for the 7 diploid hybrids from non-tuber-bearing diploid species *S. etuberosum* × Mexican diploid species *S. pinnatisectum* are found in certain *Solanum* diploid hybrids. They have reported that the above hybrids had mean pairing frequencies of $0.02\sim0.05_{\mathrm{III}}+2.83\sim4.11_{\mathrm{II}}+15.68\sim18.28_{\mathrm{I}}$ at metaphase I and a very low pollen fertility (below 10%). On the basis of such a view, the genomes of the *COM* and *TUB* diploid species should be considered, as pointed out already by the present author[12,13] and other workers [3,6], to belong to the same genome category, even if there exist some structural differences between the chromosomes of both genomes.

From the considerations mentioned above, the following conclusions may be drawn: 1) the genomes of all the *COM* diploid species, except *cmm*, are highly homologous with one another, but the genome of *cmm* is slightly differentiated from, though similar to, them; 2) likewise, the genomes of all the *TUB* diploid species are also highly homologous with one another; 3) the *COM* and *TUB* diploid species are closely related to each other by their possession of homologous genomes; and 4) thus, the genomes of all the diploid species used are symbolized as AA, following the genome symbol proposed by earlier workers for these species[3,6,12,13,15].

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バレイショ近縁種における種の分化

XII. *Commersoniana* 群2倍種と*Tuberosa* 群2倍種の群内及び群間のゲノム類縁関係

松　林　元　一

要　約

Commersoniana (*COM*) 群野生2倍種4種，*Tuberosa* (*TUB*) 群野生2倍種2種，同群栽培2倍種3種及び *S. tuberosum* の2倍性半数体 (*tbr*-2x) (以上いずれも 2n=24) を用い，相互間におけるゲノムの類縁関係を明らかにするために，2倍種間の交雑能力を調べ，さらに2倍雑種，複2倍体及びそれらの両親同質4倍体の細胞遺伝学的行動を観察した。得られた結果を次に要約する。

1) *COM* 群2倍種は，*S. commersonii* (*cmm*) を除いて，相互に高い交雑能力を示した。2倍雑種は，*cmm* 関与のもの以外，いずれも第1中期で観察細胞数の96%以上が規則的な染色体対合12_{II}を示し，第1後期と第2中期の染色体行動にも特記すべき異常はみられず，花粉も90%以上が正常であった。 *cmm* 関与の雑種には，移動期に4連染色体の形成，第1後期に遅滞染色体や染色体橋等の異常が現われ，花粉稔性も70%前後であった。複2倍体の多価頻度は，両親同質4倍体のそれに比べ，有意的に低い値を示した *cmm* 関与のものを除き，すべて高い値を示した。

2) *TUB* 群2倍種も相互間の交雑は容易であったが，交雑能力は *COM* 群のそれより低かった。2倍雑種では，いずれも90%前後の細胞が12_{II} を示し，以後の染色体行動は一般に正常であった。花粉は *tbr*-2x 関与の雑種(27.6%)以外いずれも70〜80%が正常であった。複2倍体は両親同質4倍体よりもむしろ高い頻度で多価形成を示した。

3) 前記両群2倍種の群間交雑は容易であったが，交雑能力は群内の場合に比してやや低かった。2倍雑種の第1中期では80%前後の細胞が12_{II} を示した。しかし，異形対合の出現に加え，第1後期以後には遅滞染色体，染色体橋，分散染色体等の異常が群内雑種よりやや高頻度でみられた。稔性は良好で *TUB* 群内雑種と大差なかった。複2倍体は，群内複2倍体と異なって，両親同質4倍体に比べ多価頻度の有意的な低下を示した。

4) 以上の結果から次の見解が導かれた。i) *COM* 群2倍種はいずれも相同ゲノムを共有するが，*cmm* のゲノムには若干の構造的分化がみられる。ii) *TUB* 群2倍種のゲノムも互いに相同である。 iii)両群2倍種のゲノム間には，複2倍体における選択対合によって検出できる程度の構造的差異が存在するが，それはゲノムのカテゴリーを異にするほど大きいものではない。したがって，両群2倍種のゲノム型は，従来の提案どおりAAと記号づけるのが妥当と考えられる。