Fertility of Autotetraploids and Their Hybrids in Barley, II

Meiosis and Fertility in Tetraploid Hybrids

Takumi TSUCHIYA

Reprinted from SEIKEN ZIHÔ, Report of the
Kihara Institute for Biological Research
No. 8, Dec. 1957

財団法人　木原生物学研究所　**生研時報**　第 8 号　別刷
昭和 32 年 12 月 30 日発行

Fertility of Autotetraploids and Their Hybrids in Barley, II

Meiosis and Fertility in Tetraploid Hybrids

Takumi TSUCHIYA

Kihara Institute for Biological Research, Yokohama

Increase of fertility in hybrids between induced autotetraploids has been reported by MÜNTZING (1939, 1943) in *Galeopsis*, SKIRM (1940, 1942) in *Tradescantia*, SPARROW *et al.* (1942) in *Antirrhinum*, RANDOLPH (1942) in *Zea*, CUA (1952) in *Oryza*, and MÜNTZING (1948) in *Hordeum*.

The hybrids used in the present investigation were obtained from reciprocal crosses between induced autotetraploids of *Hordeum spontaneum* C. KOCH var. *transcaspicum* VAV.[1] and Early Golden Melon (*H. sativum*). Aceto-carmine preparations were used for the observations of meiotic chromosomes in PMC and pollen analysis.

The author wishes to express his sincere thanks to Dr. H. KIHARA, Director of National Institute of Genetics, Misima, Japan, for his kind guidance and encouragement in the course of this investigation. The present manuscript was kindly revised by Dr. K. YAMASHITA, Professor of Kyoto University, to whom are due the author's cordial thanks.

Meiosis in eutetraploid hybrids

At diakinesis and MI in the tetraploid hybrids with $2n=28$, quadrivalents, trivalents, bivalents and univalents were observed. All the configurations were derivatives of 7_{IV} (Tab. 1 and Figs. 1, 3, 4). The number of quadrivalents and univalents per PMC and the frequency of PMC with univalents are given in Tables 1 and 3.

In the tetraploid hybrids a few PMC without quadrivalents were observed (Tab. 1), while in the induced autotetraploid plants all the analyzed PMC had one or more quadrivalents (cf. TSUCHIYA 1953b). Various types of quadrivalents were observed at MI: zig-zag, chain, O-type, ring-and-rod and others (Figs. 1–4). The meiotic behavior of the eutetraploid hybrids was similar to that of induced autotetraploids. Lagging chromosomes and chromosome bridges were frequently met with at AI, TI, AII and TII. Accordingly, micronuclei and extra microcells were found at interkinesis and tetrad stage (cf. TSUCHIYA 1953b).

Meiosis in a hypotetraploid hybrid

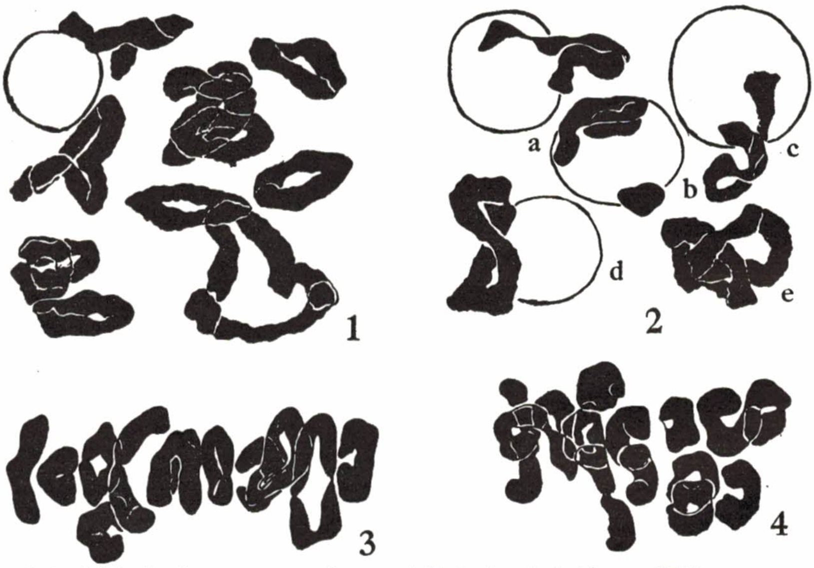
At MI in a hypotetraploid hybrid with $2n=27$, various configurations with varying number of quadrivalents, trivalents, bivalents and univalents were observed (Tab. 2).

1) This species was described in the first paper of this series as *Hordeum spontaneum nigrum*.

Table 1. Chromosome configurations at MI in the eutetraploid hybrids ($2n=28$)

Chromosome configurations				Number of PMC*	Number of			
IV	III	II	I		IV	III	II	I
6		2		3	18		6	
5		4		13	65		52	
5		3	2	1	5		3	2
4	1	4	1	2	8	2	8	2
4		6		9	36		54	
4		5	2	2	8		10	4
3	1	6	1	1	3	1	6	1
3		8		17	51		136	
3		7	2	2	6		14	4
2	1	8	1	2	4	2	16	2
2		10		11	22		110	
2		9	2	4	8		36	8
1	1	10	1	3	3	3	30	3
1		12		9	9		108	
	1	12	1	1		1	12	1
		14		1			14	
		13	2	1			13	2
Total				82	246	9	628	29
Frequency per PMC					3.00	0.1	7.66	0.35

* A total observed in 8 F_1 plants obtained from the reciprocal crosses of *H. spontaneum* var. *transcaspicum* 4*x* × Early Golden Melon 4*x*.



Figs. 1–4. Meiotic chromosomes of tetraploid barley hybrids. ×1700.
1, $3_{IV}+8_{II}$ in an eutetraploid hybrid (18–26), showing a nucleolus attached to one bivalent. 2a–d, nucleolus-chromosome relationships in the same hybrid (18–26). 2e, interlocked two quadrivalents in another hybrid (18–20). 3, $3_{IV}+8_{II}$ at MI in 18–23. 4, $2_{IV}+10_{II}$ at MI in 18–15.

The frequency of trivalents and univalents was very high in comparison with the above mentioned tetraploid hybrids with $2n=28$ (Tabs. 1–3).

Table 2. Chromosome configurations at MI in the hypotetraploid hybrid ($2n=27$)

Chromosome configurations				Number of PMC	Number of			
IV	III	II	I		IV	III	II	I
5	1	2		1	5	1	2	
5		3	1	2	10		6	2
4	1	4		4	16	4	16	
4	1	3	2	2	8	2	6	4
4		5	1	2	8		10	2
3	2	4	1	1	3	2	4	1
3	1	6		4	12	4	24	
3		7	1	2	6		14	2
3		6	3	1	3		6	3
2	1	8		5	10	5	40	
2		9	1	4	8		36	4
1	1	10		1	1	1	10	
1		11	1	1	1		11	1
1		10	3	1	1		10	3
	1	12		1		1	12	
Total				32	92	20	207	22
Frequency per PMC					2.9	0.6	6.5	0.7

The number of univalents and quadrivalents per PMC and the frequency of PMC with univalents are given in Tables 2 and 3. The average of trivalents per PMC was 0.63 in the hypotetraploid hybrid, while it was 0.11 in eutetraploid hybrids. The frequency of PMC with trivalents was 59.37% in the former, and 10.98% in the latter. In all 32 PMC analyzed occurred trivalents or univalents or both; they are considered to be the main causes of meiotic irregularities and reduction in fertility. The trivalents were all chains, as diagramatically shown by ∨, √ or ⋮.

The number of quadrivalents per PMC of the hypotetraploid hybrid is equal to that found in the eutetraploid hybrid plants (Tab. 3). But it is less than that of one of the parents, *H. spontaneum* var. *transcaspicum*. The meiotic behavior of chromosomes was similar to that of the induced autotetraploids and the eutetraploid hybrids mentioned above (cf. TSUCHIYA 1953a). At AI in the hypotetraploid hybrid, about 82% of the PMC have one or more laggards or chromosome bridges. The lagging chromosomes were found in 51.9% of PMC at TI. The percentage of PMC with micronuclei or extra microcells at interkinesis was 34.6%. The second meiotic division was also irregular showing abnormal nuclear plates at MII (83.5%), laggards at AII and TII (70.8%). Triads, pollen tetrads with micronuclei and other abnormalities occurred at tetrad stage (45%).

Fertility

Abnormalities found in the pollen grains of two kinds of tetraploid hybrids, $2n=$ 28 and 27, were similar and also the same as those in the induced autotetraploid barley (cf. TSUCHIYA 1953a). Various degrees of degeneration of pollen grains were observed.

The pollen and seed fertility in the tetraploid hybrids are shown in Table 3. It

Table 3. Chromosome behaviors and fertilities in tetraploid barley hybrids and the parents

Materials	Frequency of			Fertility		
	quadriv. per PMC	unival. per PMC	PMC with univ. (%)	pollen	seed: self	seed: free
H. spont. transcasp. $4x$	4.28±0.73	0.06	5.55	84.86	51.04	57.34
Eu-$4x$ hybrid $2n=28$	3.00±1.03	0.36	23.17	94.24	78.33	80.28
Hypo-$4x$ hybrid $2n=27$	2.88±0.83	0.69	50.00	94.94	77.07	77.60
Early Golden Melon $4x$	3.41±0.88	0.14	9.80	82.44	77.45	81.57

is noteworthy that no remarkable difference was detected in pollen and seed fertility between eu- and hypo-tetraploid hybrids, though the former had less univalents and the latter more univalents and trivalents.

Discussion

The seed fertility of autotetraploid Early Golden Melon (77.5 %) was higher than that of autotetraploid *Hordeum spontaneum* C. KOCH var. *transcaspicum* VAV. (51.0 %) (cf. ONO 1949a, 1952; TSUCHIYA 1953a). The frequency of quadrivalents at MI was lower in the former (3.41±0.88) than in the latter (4.28±0.73). Therefore, the low fertility of autotetraploid *H. spontaneum* var. *transcaspicum* seems to be partly due to the high frequency of quadrivalents at MI (TSUCHIYA 1953a; cf. DARLINGTON 1937). The eutetraploid hybrids between the two autotetraploid barleys mentioned above showed nearly the same pollen and seed fertility and the same frequency of quadrivalents as autotetraploid Early Golden Melon, one of the parents of the tetraploid hybrids (Tab. 3).

These results suggest that there is a correlation between the seed fertility and the frequency of quadrivalents at MI. Similar results have been reported for autotetraploid rice varieties and their hybrids by CUA (1952), MASIMA (1952) and MASIMA and UCHIYAMADA (1955).

MYERS (1945) and MYERS and HILL (1941, 1942, 1943), however, stated that no correlation was found between the fertility and the frequency of quadrivalents at MI and between the frequency of laggards at AI and micronuclei at tetrad stage in several induced and natural autotetraploid forage grasses. They also emphasized that there are positive correlations between the frequency of PMC with univalents at MI and AI with laggards, between MI with univalents and tetrads with micronuclei, and between AI with laggards and tetrads with micronuclei. This was supported by MASIMA's findings (MASIMA 1947) in autotetraploid and hypotetraploid *Linum angustifolium* HUDS.

Among the sibs of tetraploid hybrids the present author found a hypotetraploid plant ($2n=27$) which showed many univalents at MI. No difference was detected between the hypotetraploid hybrid plant and the eutetraploid hybrids in pollen- and seed-fertility and in the frequency of quadrivalents at MI (Tab. 3). However, the frequency of univalents at MI differed rather widely in different materials (cf. Tab. 3 and TSUCHIYA 1953b). In the eutetraploid hybrids 0.36 univalents per PMC were found, while in the hypotetraploid hybrid the frequency of univalents was about twice as high as in the eutetraploid hybrids, *i.e.* 0.69 per PMC. These results seem to indicate that there is no correlation between seed- or pollen-fertility and the frequency of univalents at MI, and that the sterility becomes higher in proportion to the frequency of quadrivalents at MI.

Summary

The author studied the meiosis and fertility of tetraploid barley hybrids produced by reciprocal crosses between *Hordeum spontaneum* C. KOCH var. *transcaspicum* VAV. $4x$ and Early Golden Melon $4x$. The results are summarized as follows:

1. At diakinesis and MI in the PMC of the eutetraploid hybrids with $2n=28$, various configurations with varying number of quadrivalents, trivalents, bivalents and univalents were observed. The number of quadrivalents per PMC varied from 0 to 6 with an average of 3.00 ± 1.03. The frequency of univalents was 0 to 2 with an average of 0.35 per PMC.

2. At MI in a hypotetraploid hybrid ($2n=27$) various configurations with varying number of quadrivalents, trivalents, bivalents and univalents were also found. The frequency of trivalents and univalents was very high in comparison with the eutetraploid hybrids; the average number of univalents per PMC was 0.7 and that of trivalents was 0.6.

3. The process of meiosis in the tetraploid hybrids was similar to that found in the induced autotetraploids. Lagging chromosomes and chromosome bridges were observed in both first and second meiotic divisions and micronuclei and extra microcells were observed at interkinesis and tetrad stage.

4. No remarkable differences were detected in pollen- and seed-fertility between eu- and hypo-tetraploid hybrids.

5. The results mentioned above seem to indicate that there is no correlation between seed- or pollen-fertility and the frequency of univalents at MI, and that the sterility becomes higher in proportion to the frequency of quadrivalents at MI.

Literature cited

CUA, L. D. 1952. Artificial polyploidy in the *Oryzeae*, III. Cytogenetical studies on intra- and inter-subspecies tetraploid hybrids in *Oryza sativa* L. Seiken Zihô **5**: 42–53.

DARLINGTON, C. D. 1937. Recent advances in cytology, 2nd ed., Blakiston, Phila. 671 pp.

MASIMA, I. 1947. Meiosis in diploid and tetraploid plants of *Linum angustifolium* HUDS. Cytologia **14**: 55–69.

——— 1952. Causes of sterility in tetraploid rice. (in Jap. with Eng. rés.) Jap. Jour. Breed. **1**: 179–188.

——— and UCHIYAMADA, H. 1955. Studies on the breeding of fertile tetraploid plants of rice. (in Jap. with Eng. rés.) Bull. Nat. Inst. Agric. Sci. (Japan) Ser. D, **5**: 104–136.

MÜNTZING, A. 1939. Incompatibility and fertility in experimental and natural polyploids. Proc. 7th Intern. Cong., Edinburgh, 1939: 224.

——— 1943. Fertility improvement by recombination in autotetraploid *Galeopsis pubescens*. Hereditas **29**: 201–204.

——— 1948. Experiences from work with induced polyploidy in cereals. Svalöf 1886–1946: 324–337.

MYERS, W. M. 1945. Meiosis in autotetraploid *Lolium perenne* in relation to chromosomal behavior in autotetraploids. Bot. Gaz. **106**: 304–316.

——— and HILL, H. D. 1941. Studies of chromosomal association and behavior and occurrence of aneuploidy in autotetraploid grass species, orchard grass, tall oat grass, and crested wheatgrass. *Ibid*. **102**: 236–255.

——— and ——— 1942. Variations in chromosomal association and behavior during meiosis among plants from open-pollinated populations of *Dactylis glomerata*. *Ibid*. **104**: 171–177.

——— and ——— 1943. Increased meiotic irregularity accompanying inbreeding in *Dactylis glomerata* L. Genetics **28**: 383–397.

ONO, T. 1949a. Fertility of the tetraploid barley. (in Jap.) Jap. Jour. Genet. **24**: 81–82.

——— 1949b. Studies on polyploid barley. (in Jap.) Jap. Jour. Genet. Suppl. **2**: 75–77.

——— 1952. Studies on tetraploid barley artificially induced. (in Jap. with Eng. rés.) Papers Coord. Commit. Res. Genet. **3**: 67–70.

RANDOLPH, L. F. 1942. The influence of heterozygosis on fertility and vigor in autotetraploid maize. Genetics **27**: 163.

SKIRM, G. W. 1940. Frequency of quadrivalent formation in *Tradescantia* tetraploids. *Ibid*. **25**: 136–137.

——— 1942. Bivalent pairing in an induced tetraploid of *Tradescantia*. *Ibid*. **27**: 635–640.

SPARROW, A. H., RUTTLE, M. and NEBEL, B. R. 1942. Comparative cytology of sterile intra- and inter-varietal tetraploids of *Antirrhinum majus* L. Amer. Jour. Bot. **29**: 711–715.

TSUCHIYA, T. 1953a. Fertility of autotetraploids and their hybrids in barley, I. Meiosis and fertility in some autotetraploids. Seiken Zihô **6**: 46–52.

——— 1953b. Cytogenetic investigations of twin plants occurred in a tetraploid barley hybrid. *Ibid*. **6**: 53–56.

PRINTED BY
KOKUSAI BUNKEN INSATSUSHA
CHIYODA-KU, TOKYO