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Takumi TSUCHIYA

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Meiosis and fertility in some autoteraploids[1]

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The relation between fertility and chromosome behavior during meiosis in induced autotetraploids has been an important problem. Though induced autotetraploids in barley have been studied by several authors (Peto 1936, Müntzing et alii 1937, Karpechenko 1938, Dorsey 1939, Greis 1940, Smith 1942, Chen et alii 1945, Ono 1946, 1947, 1948, 1949 a, b, 1952), no detailed reports have been published on the cause of the reduction in fertility of autotetraploid plants. The author carried out an investigation of meiosis and fertility in barley autotetraploids and their hybrids, and the results are briefly described in this paper.

Materials and methods

The materials used in the present investigations are as follows:

Early Golden Melon (a cultivated two-rowed variety of *Hordeum sativum*), $2x$ and $4x$.

Hosokara No. 2 (a six-rowed cultivated variety of *H. sativum*), $2x$ and $4x$.

H. spontaneum nigrum (two-rowed wild species), $2x$ and $4x$.

The autotetraploid plants which were used in the present investigation were originally produced by Dr. T. Ono, Professor of Tōhoku University (Ono 1946, 1947).

Temporary aceto-carmine preparations were exclusively used for the observation of meiosis and the determination of pollen fertility.

Meiosis

So far investigated in the diploids seven bivalents have been seen at first meiotic metaphase and no abnormalities have been observed throughout the meiosis.

In the autotetraploids, at diakinesis quadrivalents and bivalents were frequently observed (Fig. 1), while trivalents and univalents occurred rarely. Various types of quadrivalents occurred, such as zig-zag, chain, open-ring and flying pan (Fig. 2).

As shown in Table 1 and Figures 3 to 6, the chromosome configuration at IM was either 7_{IV} or its derivatives, varying in the number of quadrivalents, trivalents, bivalents and univalents. No quinquevalent or higher associations were observed.

The results of the quadrivalent analysis at IM in the autotetraploids are shown in

1) Contributions from the Laboratory of Genetics, Biological Institute, Kyoto University, No. 252

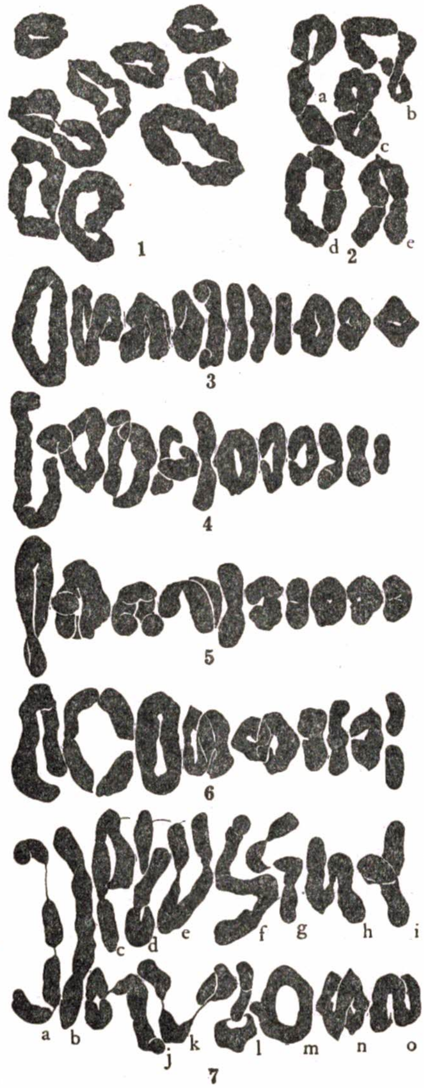
Table 2. From the table we can see that the frequency of quadrivalents per sporocyte in Early Golden Melon is lower than in other varieties.

At first metaphase various types of quadrivalents were observed, as shown in Table 3 and Figures 3 to 7. Zig-zag and O-types were most commonly observed, N and other types being met infrequently.

The number of univalents per sporocyte and the frequency of sporocytes with univalents are shown in Table 4. The frequency of sporocytes with univalents was highest in Hosokara No. 2 (26.08 %, 1948) and very low in Early Golden Melon (9.80 %) and in *H. spont. nigrum* (5.55 %).

The meiotic behavior of chromosomes from IA to the quartet stage was similar in all three autotetraploids and various sorts of abnormalities were observed. At IA 1~7 lagging chromosomes occurred which were distributed to the poles as undivided dyads or monads (divided halves), or they lagged behind at IT. At interkinesis, micronuclei, chromosome bridges and sporocytes with 1 or 2 micro-cells besides normal daughter cells were met. Irregular nuclear plates were observed at IIM. At quartet stage, tetrads with micronuclei and pentads besides normal tetrads were most frequently observed, and dyads, triads and sporocytes with 5~9 cells occurred, but not frequently.

In Hosokara No. 2 (1947) the percentages of abnormal sporocytes observed in various stages were as follows :



Figs. 1~7 Meiotic chromosomes in induced autotetraploids of barley

1 Diakinesis showing $5_{IV}+4_{II}$, 2 Diakinetic quadrivalents, 3~7 First metaphase chromosomes, 3 $3_{IV}+8_{II}$, 4 $3_{IV}+1_{III}+6_{II}+1_{I}$, 5 $4_{IV}+6_{II}$, 6 $5_{IV}+3_{II}+2_{I}$, 7 Several instances of IM quadrivalents ×1630

1 and 2 Early Golden Melon, 3, 7 a, c~h, k~m and o, *H. spont. nigrum*, 4~6, 7 b, i, j and n, Hosokara No. 2

26.74 % at IA~IT, 26.66 % at interkinesis, 39.13 % at IM (polar view), 39.38 % at IIA~IIT, and 54.74 % at the quartet stage. They are higher than that of sporocytes with univalents at IM (13.43 %). The number of lagging chromosomes at IA~IT ranged from 0 to 7 with an average of 0.47 per sporocyte, which was also higher than that of the univalents at IM, ranging from 0 to 4 with the average of 0.22 (Table 4).

Table 1 Chromosome configurations at first meiotic metaphase in induced autotetraploid barleys

Configurations with varying number of				Number of sporocytes observed			
IV	III	II	I	Hosokara 1947	No. 2 1948	Early Golden Melon 1948	*H. spont. nigrum* 1948
7				4		1	
6	1		1	1			
6		2		18	4	2	3
6		1	2	3			
5	1	2	1	1			1
5		4		32	3	5	3
5		3	2	1	2		
4	1	4	1	4		1	
4	1	3	3	1			
4		6		39	7	16	7
4		5	2	1			
3	1	6	1	3	2		
3		8		15	3	13	3
3		7	2	1	1		
3		6	4	1			
2	2	6	2			1	
2	1	8	1	1		1	
2		10		6		6	1
2		9	2			1	
1	1	10	1			1	
1		12		2		3	
1		11	2		1		
Total				134	23	51	18

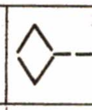
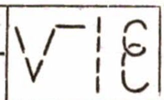
Table 2 Frequency of quadrivalents at first meiotic metaphase in induced autotetraploid barleys

Materials	Frequency of sporocytes with quadrivalents								
	1	2	3	4	5	6	7	Total	M ± m
Hosokara No. 2 1947	2	7	20	45	34	22	4	134	4.37±0.11
〃 1948	1	0	6	7	5	4	0	23	4.17±0.26
E. G. Melon 1948	4	9	13	17	5	2	1	51	3.39±0.19
H. spont. nigr. 1948	0	1	3	7	4	3	0	18	4.28±0.24

Fertility

The pollen fertility was higher in diploids than in autotetraploids (Table 5) which

Table 3 Types of quadrivalents and their frequencies in induced autotetraploid barleys

Materials	Types						Total
							
Hosokara No. 2 1947	222	314	0	—	0	42	578
〃 1948	37	47	7	4	3	5	103
E. G. Melon 1948	91	46	1	28	4	4	174
H. spont. nigr. 1948	22	30	1	5	2	4	64

1) In the data for Hosokara No. 2 (1947), the type of is included in , both being treated as open-rings.

Table 4 Frequency of univalent chromosomes at first meiotic metaphase in induced autotetraploid barleys

Materials	Frequency of univalents per sporocyte (aver.)	Number of sporocytes		
		without univalents (%)	with univalents (%)	Total
Hosokara No. 2 1947	0-4 (0.22)	116 (86.56)	18 (13.43)	134
〃 1948	0-2 (0.43)	17 (73.91)	6 (26.08)	23
E. G. Melon 1948	0-2 (0.14)	46 (90.19)	5 (9.80)	51
H. spont. nigr. 1948	0-1 (0.06)	17 (94.44)	1 (5.55)	18

Table 5 Fertility of artificial autotetraploids in barley, compared with the diploids

Materials	Pollen fertility				Seed fertility (%)	
	Total number	Normal (%)	Degene-rated	Empty	Selfed	Free
Hosokara No. 2						
(1947) $4x$	1200	895 (74.59)	305*		53.67	49.63
〃 $2x$	1499	1456 (97.13)	43*		94-06	93.22
〃 (1948) $4x$	2834	2202 (77.69)	321	311	—	—
〃 $2x$	956	914 (95.60)	5	37	—	—
E. G. Melon						
$4x$	638	526 (82.44)	59	53	77.45	81.57
〃 $2x$	1184	1154 (97.46)	24	6	95.48	97.97
H. spont. nigr.						
$4x$	1664	1412 (84.86)	207	45	51.04	57.34
〃 $2x$	704	701 (99.57)	2	1	93.41	92.98

* This number shows the total of degenerated and empty pollen grains

showed no remarkable differences between the varieties, while Hosokara No. 2 seemed to have a somewhat lower percentage of good pollen than the others.

In diploid plants seed-fertilities were 93 % for both Hosokara No. 2 (1947) and *H. spon. nigrum* and about 98 % for Early Golden Melon, while in the autotetraploid varieties the seed-fertilities were about 50 % for the former 2 varieties when bagged or open-pollinated, and for Early Golden Melon 77.45 % when self-pollinated and 81.57 % when open-pollinated.

Discussion

It is well known that the occurrence of quadrivalents in autotetraploids gives rise to meiotic irregularities. In barley Chen et alii (1945) stated that the autotetraploid plants with multivalents at IM (their group 4) showed abnormal separation at IA followed by the formation of defective gametes and reduction in fertility. Karpechenko (1938) also reported a similar phenomenon in autotetraploid barley. In the autotetraploids in which none or a few quadrivalents were found the meiosis proceeded regularly. According to Chen et alii (1945) the induced autotetraploid plants in barley with 14 bivalents at IM (Group 5) had regular meiosis and rather high fertility.

Randolph (1935), however, reported that the meiotic process in the autotetraploid maize is rather regular, though 7~9 quadrivalents per sporocyte were found at first meiotic metaphase.

The frequency of quadrivalents per sporocyte was nearly the same in Hosokara No. 2 (1947, 1948) and *H. spont. nigrum*, while it was lower in Early Golden Melon (Table 2). The frequency of univalents per sporocyte and also the number of sporocytes with univalents in Early Golden Melon were lower than in the other varieties, as shown in Table 4. The high fertility of Early Golden Melon compared with the other varieties might be partly ascribed to these facts.

In Hosokara No. 2 (1947) the percentage of sporocytes with laggards at IA~IT is higher than expected from the number of univalents at IM. Therefore, the quadrivalents should be also considered as the source of IA-laggards. Myers (1945), however, stated that there was no correlation between the frequency of quadrivalents and the meiotic irregularities and that the occurrence of univalents was the main cause of meiotic abnormalities in autotetraploids.

The seed-fertility of Early Golden Melon was remarkably higher than in other varieties, as reported by Ono (1946, 1947, 1948, 1949 a, b, 1952), though the pollen-fertility was nearly the same in all varieties (Table 5). A seed-fertility of about 50 % was obtained in Hosokara No. 2 (1947, 1948) and *H. spont. nigrum*, while the pollen-fertiliy was 75-78 % for the former and 85 % for the latter. To clarify the relation between the frequency of quadrivalents and the pollen as well as seed-fertilities further studies are required.

Summary

Meiosis and fertility of induced autotetraploids of the barley varieties, Early Golden Melon, Hosokara No. 2 and *H. spontaneum nigrum*, were investigated and compared with the respective diploids. The results are summarized as follows :

1. In the diploids meiosis proceeded regularly and resulted in high fertility.

2. At diakinesis and IM in the induced autotetraploids, varying numbers of quadrivalents, trivalents, bivalents and univalents were observed, the configurations being either 7_{IV} or its derivatives. Various types of quadrivalents were recorded at diakinesis and IM, such as chain, zig-zag, open-ring and flying pans, among which the types of zig-zag and open-ring were most commonly observed.

3. The average number of univalents per sporocyte at IM was 0.22 (1947) and 0.43 (1948) in Hosokara No. 2, 0.14 in Early Golden Melon and 0.06 in *H. spont. nigrum.* The frequency of sporocytes with univalents at IM was high in Hosokara No. 2 (26.08 % in 1948) and low in Early Golden Melon (9.80 %) and in *H. spont. nigrum* (5.55%).

4. At the stages between IA and quartet formation, various abnormalities were observed. Lagging chromosomes and chromosome bridges were seen at IA~IT and IIA~IIT. Micronuclei were found at interkinesis and quartet stage, and also sporocytes with 3~4 cells (interkinesis) and 2, 3, 5~9 cells (quartet) were observed, but not frequently.

5. In autotetraploid Hosakara No. 2, the percentages of abnormal sporocytes at the stages from IA to quartet were higher than that of sporocytes with univalents at IM, and the number of laggards at IA~IT was also higher than that of univalents at IM.

6. The pollen- and seed-fertilities were higher in diploids than in the induced autotetraploids. The seed-fertility of autotetraploid Early Golden Melon was higher than in the other varieties.

7. Some considerations were made on the relation between IM-configurations and abnormalities occurring at the stages from IA to quartet.

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