Studies on X-ray induced reciprocal translocations in Einkorn wheats. III.

A newly synthesized ring of 14 chromosomes in a complex

heterozygote, *aegilopoides* · *monococcum*¹

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Introduction

As previously reported (Yamashita, 1950 b), an analysis of X-ray induced reciprocal translocations (RT) in Einkorn wheats was carried out and a series of the following six RT-types, involving all seven chromosomes, was established, namely a-b, b-c, c-d, d-e, e-f, and f-g (Fig. 5). The seven chromosomes were designated as a, b, c, d, e, f and g, and the RT's between them as a-b, b-c and so forth.

In the attempts to combine the chromosomes into larger rings, carefully planned successive crosses among the established RT-types have been systematically carried out, and at last, this year, the synthesis of a ring of 14 chromosomes was achieved. Thus, all possible combinations of rings and pairs, obtainable from the 14 Einkorn chromosomes, were realized, resulting in a complete series of structural hybrids comparable with the well known situation in *Oenothera* (Tab. 1). The results of this investigation were partly reported in the previous paper (Yamashita 1950c).

Table 1. Combinations of pairs and rings induced and synthesized in Einkorn wheats and found in *Oenothera*.

Original 7II		
④	+5II	⑧ +3II
④+④	+3II	⑧+④+1II
④+④+④	+1II	⑧+⑥
⑥	+4II	⑩ +2II
⑥+④	+2II	⑩+④
⑥+④+④		⑫ +1II
⑥+⑥	+1II	⑭

A figure within a circle indicates the number of chromosomes involved in a ring.

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The experiments were carried out under the guidance of Dr. Hitoshi Kihara to whom I wish to express my heartiest thanks. I also wish to tender my thanks to the Ministry of Education for the economic assistance.

Material and methods

Two species of Einkorn were used, i.e. *Triticum aegilopoides* Bal. var. *boeoticum* Perc. and *T. monococcum* L. var. *vulgare* Koern. The genomes of both species are homologous, and the chromosomes show

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normal conjugation in their fully fertile hybrids. As Table 2 shows, 16 RT-types were obtained from various experiments with X-ray treatments of dormant seeds of the two species. Some of the RT's were found in heterozygous condition in X_1 (i.e. first generation from the X-ray treated seeds), others were found in homozygous condition in later generations. The detailed pedigrees of the materials were given in the previous paper (Yamashita, 1950b).

Table 2. Reciprocal translocations induced by X-rays in Einkorn wheats

Sources	<i>T. aegilopoides</i>	<i>T. monococcum</i>
Treatment in		
1939	5: aT1, aT2, aT3, aT4, aT5	2: mT1, mT2
1943		5: mT3, mT4, mT5, mT8, mT9
1946	2: aT6, aT7	2: mT6, mT7

For the observation of meiosis in the PMC's acetocarmine smear preparations were used. The microphotograph shown in Fig. 4b was taken by the phase contrast microscope through the kind offices of Dr. Kenji Nakamura to whom I wish to express here my thanks.

Analysis of reciprocal translocations

The mechanism of ring formation is adequately explained by the well known assumption of segmental interchanges. For instance, when an interchange occurs between two non-homologous chromosomes, $\begin{smallmatrix} 1 \\ \text{---} \\ 2 \end{smallmatrix}$ and $\begin{smallmatrix} 3 \\ \text{---} \\ 4 \end{smallmatrix}$, resulting in $\begin{smallmatrix} 1 \\ \text{---} \\ 3 \end{smallmatrix}$ and $\begin{smallmatrix} 2 \\ \text{---} \\ 4 \end{smallmatrix}$, the corresponding segments will pair in the heterozygotes, and a ring of 4 chromosomes will be formed: $\begin{smallmatrix} 1 \\ \text{---} \\ 3 \end{smallmatrix} \times \begin{smallmatrix} 2 \\ \text{---} \\ 4 \end{smallmatrix} = \begin{smallmatrix} a-b \\ a \quad b \end{smallmatrix}$ (Fig. 1).

Fig. 1. Schema showing the meiotic behavior of ④. a, Two pairs of non-homologous chromosomes, $\begin{smallmatrix} 1 \\ \text{---} \\ 2 \end{smallmatrix}$ and $\begin{smallmatrix} 3 \\ \text{---} \\ 4 \end{smallmatrix}$. b, Pachytene figure in an RT-heterozygote: A and C represent the interchanged chromosomes and B and D represent the original ones. c, Zigzag arrangement. d, O-arrangement.

As an Einkorn-genome is composed of 7 non-homologous chromosomes, from the random combinations of 2 non-homologous chromosomes 21 different RT-combinations can be expected.

The analysis of the induced RT's was planned and carried out according to the following general rules on which my working methods had been based.

1. If in the hybrid between 2 RT-types the RT's are of the same constitution, the involved chromosomes will pair normally, e.g. $\frac{1}{1} \frac{2}{2} \frac{3}{3} \frac{4}{4}$. 2. If in the hybrid the involved chromosomes are the same but have a different segmental arrangement, a ring of 4 chromosomes will be produced, e.g. $\frac{1}{1} \frac{2}{2} \frac{3}{3} \frac{4}{4} \times \frac{1}{1} \frac{2}{2} \frac{3}{3} \frac{4}{4}$. 3. If two RT-types have one chromosome in common, a ring of 6 chromosomes will be formed in the hybrid, e.g. $\frac{1}{1} \frac{2}{2} \frac{3}{3} \frac{4}{4} \times \frac{1}{1} \frac{2}{2} \frac{3}{3} \frac{4}{4} \times \frac{1}{1} \frac{2}{2} \frac{3}{3} \frac{4}{4} = \frac{a-b}{a} \frac{c}{b-c}$. 4. If the segmental relations in the case of 2 RT-types are quite different, 2 rings of 4 chromosomes will be produced in the hybrid, e.g. $\frac{1}{1} \frac{2}{2} \frac{3}{3} \frac{4}{4} \times \frac{1}{1} \frac{2}{2} \frac{3}{3} \frac{4}{4} + \frac{5}{5} \frac{6}{6} \frac{7}{7} \frac{8}{8} \times \frac{5}{5} \frac{6}{6} \frac{7}{7} \frac{8}{8} = \frac{a-b}{a} \frac{c}{b} \frac{d}{c-d}$.

The results of the crossing experiments between the induced RT's obtained from the treatment in 1939 are shown in the following table (Tab. 3).

Table 3. Ring configurations in the hybrids between RT-types

$aT1 \times aT2 = \textcircled{6}$				
$\times aT5 = \textcircled{4} + \textcircled{4}$	$aT2 \times aT5 = \textcircled{6}$			
$\times mT2 = \textcircled{4} + \textcircled{4}$	$\times mT2 = \textcircled{4} + \textcircled{4}$	$aT5 \times mT2 = \textcircled{6}$		
$\times aT3 = \textcircled{4} + \textcircled{4}$	$\times aT3 = \textcircled{4} + \textcircled{4}$	$\times aT3 = \textcircled{4} + \textcircled{4}$	$mT2 \times aT3 = \textcircled{6}$	
$\times aT4 = \textcircled{4} + \textcircled{4}$	$\times aT4 = \textcircled{4} + \textcircled{4}$	$\times aT4 = \textcircled{4} + \textcircled{4}$	$\times aT4 = \textcircled{6}$	$aT3 \times aT4 = \textcircled{6}$

From the results of these experiments the constitution formulas of the obtained first RT-types were established as follows: $aT1 = a-b$, $aT2 = b-c$, $aT5 = c-d$, $mT2 = d-e$, $aT3 = e-f$ and $aT3 = e-g$ (Yamashita, 1947-1950). These first, basic RT-types were used as testers or standards in the analysis of unknown RT's which were obtained in later experiments. The results of such an analysis are given in Tab. 4. The constitution formulas for the analyzed RT-types are given in the last column of the table.

Table 4. Analysis of some RT's which were induced later

Symbols	RT-Standards							RT-constitution formulas
	$mT5$ $a-c$	$aT1$ $a-b$	$aT2$ $b-c$	$aT5$ $c-d$	$mT2$ $d-e$	$aT3$ $e-f$	$aT4$ $e-g$	
$mT1$	—	$\textcircled{4} + \textcircled{4}$	$\textcircled{4} + \textcircled{4}$	$\textcircled{4} + \textcircled{4}$	$\textcircled{6}$	$\textcircled{4}$	$\textcircled{6}$	$e-f$
$mT3$	—	—	—	—	$\textcircled{6}$	$\textcircled{4}$	—	$e-f$
$mT4$	$\textcircled{6}$	$\textcircled{4} + \textcircled{4}$	—	—	$\textcircled{6}$	$\textcircled{6}$	—	$c-e$
$mT5^*$	—	$\textcircled{6}$	$\textcircled{6}$	$\textcircled{6}$	$\textcircled{4} + \textcircled{4}$	$\textcircled{4} + \textcircled{4}$	—	$a-c$
$mT6$	—	$\textcircled{6}$	—	—	—	$\textcircled{4} + \textcircled{4}$	$\textcircled{4} + \textcircled{4}$	$a-c, a-d, b-c \text{ or } b-d$
$mT7$	—	$\textcircled{4} + \textcircled{4}$	—	—	—	$\textcircled{6}$	—	$e-? \text{ or } f-?$
$mT8$	$\textcircled{6}$	—	$\textcircled{6}$	—	$\textcircled{4} + \textcircled{4}$	$\textcircled{6}$	—	$f-c$
$mT9$	$\textcircled{4} + \textcircled{4}$	—	$\textcircled{4} + \textcircled{4}$	—	$\textcircled{4} + \textcircled{4}$	$\textcircled{6}$	$\textcircled{6}$	$f-g$
$aT6$	—	—	$\textcircled{4} + \textcircled{4}$	—	$\textcircled{4}$	$\textcircled{6}$	$\textcircled{4} + \textcircled{4}$	$d-f$
$aT7$	—	$\textcircled{4} + \textcircled{4}$	$\textcircled{4} + \textcircled{4}$	—	7II	$\textcircled{6}$	$\textcircled{6}$	$d-e$

* $mT5 = a-c$ was also used as a standard. $mT8 \times mT9 = \textcircled{6}$.

Tab. 5 shows the results of an analysis of the meiotic configurations of a ring of 4 chromosomes derived from various RT-types. The chromosomes of a ring of four arrange themselves either disjunctionally in a zigzag or N, or non-disjunctionally in an O or U. Of course, only in the zigzag figures will the alternate chromosomes move to the opposite poles and provide each daughter cell with a complete genome. In this

Table 5. % of perfect zigzag configurations in PMC's

④ heterozygous for	aT1	82.66
	aT2	81.31
	aT3	91.37
	aT4	87.49
	aT5	75.63
	mT1	81.81
	mT2	78.57
⑫	mean.....	82.69
		22.22

manner one of the daughter cells will receive two interchanged chromosomes, while the two original chromosomes will be included into the other. Hence, in such cases, the two RT-chromosomes are always transmitted together as a set, the so called RT-set. The complete gene content of both daughter cells guarantees the production of functional gametes.

Synthesis of larger rings

As already mentioned before, ④ + ④ is produced in the hybrids between two different RT-types whose RT's have no chromosome in common. When a third RT-type is crossed with such a two-ring type, ④ + ④ + ④ will be produced, e.g. $\frac{a-b}{a} \frac{c-d}{b} \frac{e-f}{c} \frac{f}{d}$, if the third RT is quite independent of the first two. A ring of 8 will be produced, if the third RT affects a chromosome which also occurs in one of the first two, e.g. $\frac{a-b}{a} \frac{c-d}{b-c} \frac{d}{d}$. Fig. 2 shows how to combine the RT-sets; according to such plan were the crosses methodically arranged.

Fig. 2. A plan of combining RT-sets of chromosomes by successive crosses.

After many elaborate crossing experiments and painstaking analysis of the meiotic configurations, which have been carried out during 11

Table 6. Results of the crosses in 3 series A, B and C, made in 1949

A. Heterozygotes for $mT5mT2mT9$ × homozygotes for $aT1aT5aT3$ B. " " $aT2mT2mT9$ × " " "

(4)+(4)+(4)

7II

♀ gametic constitution:	♂ gametic constitution: b-a c-d e-f	Rings in the hybrids	Expected ratio	Individuals observed in the cross		
				A	B	Sum.
0	$\frac{b-a \quad c-d \quad e-f}{b \quad a \quad c \quad d \quad e \quad f}$	$= (4)+(4)+(4)$	1	2	11**	13
f-g	$\frac{b-a \quad c-d \quad e-f \quad g}{b \quad a \quad c \quad d \quad e \quad f-g}$	$= (4)+(4)+(6)$	1	4	5	9
a-c*	$\frac{b-a \quad c-d \quad e-f}{b \quad a-c \quad d \quad e \quad f}$	$= (8)+(4)$	1 } 2	7	15	22
d-e	$\frac{b-a \quad c \quad d \quad e-f}{b \quad a \quad c \quad d-e \quad f}$	$= (4)+(8)$				
a-c* f-g	$\frac{b-a \quad c-d \quad e-f \quad g}{b \quad a-c \quad d \quad e \quad f-g}$	$= (8)+(6)$	1	5	7	12
d-e f-g	$\frac{b-a \quad c-d \quad e-f \quad g}{b \quad a \quad c \quad d-e \quad f-g}$	$= (4)+(10)$	1	3	8	11
a-c* d-e	$\frac{b-a \quad c-d \quad e-f}{b \quad a-c \quad d-e \quad f}$	$= (12)$	1	2	8	10
a-c d-e f-g	$\frac{b-a \quad c-d \quad e-f \quad g}{b \quad a-c \quad d-e \quad f-g}$	$= (14)$	1	2	6	8
Total				25	60	85

C. Heterozygotes for $aT1aT5f-e-g^{***}$ × homozygotes for $aT2mT2$

(4)+(4)+(6)

7II

♀ gametic constitution:	♂ gametic constitution: b-c d-e	Rings in the hybrids	Expected ratio	Individuals observed
0	$\frac{b-c \quad d-e}{b \quad c \quad d \quad e}$	$= (4)+(4)$	1	7
a-b	$\frac{a \quad b-c \quad d-e}{a-b \quad c \quad d \quad e}$	$= (6)+(4)$	1	9
c-d	$\frac{b-c \quad d-e}{b \quad c-d \quad e}$	$= (8)$	1	11
f-e-g	$\frac{b-c \quad d-e \quad f-g}{b \quad c \quad d \quad f-e-g}$	$= (4)+(8)$	1	5
a-b f-e-g	$\frac{a \quad b-c \quad d-e \quad f-g}{a-b \quad c \quad d \quad f-e-g}$	$= (6)+(8)$	1	7
a-b c-d	$\frac{a \quad b-c \quad d-e}{a-b \quad c-d \quad e}$	$= (10)$	1	12
c-d f-e-g	$\frac{b-c \quad d-e \quad f-g}{b \quad c-d \quad f-e-g}$	$= (12)$	1	12
a-b c-d f-e-g	$\frac{a \quad b-c \quad d-e \quad f-g}{a-b \quad c-d \quad f-e-g}$	$= (14)$	1	8
Total				71

* b-c in the cross B. ** Includes 1 trisomic plant.

*** f-e-g resulted from $\frac{f-e \quad g}{f \quad e-g}$ by crossing over (Yamashita 1950b).

successive years, was the complete series of all possible types of complexes obtained. The results of three series of cross combinations arranged in 1949 are shown in Tab. 6.

The chromosome configurations at metaphase in the original type with 7 bivalents and the RT-series with ④, ⑥, ⑧, ⑩, ⑫ and ⑭ are shown in Fig. 3. Fig. 4b shows a microphotograph of ⑭ (PMC) taken from an acetocarmine preparation by the phase contrast microscope.

Figs. 3—4. Original 7II and synthesized ring-chromosomes of Einkorn wheats (metaphase I in PMC). $\times$ ca. 1000. a and b, Original 7II : *T. aestivoides*. c, ④+5II : aT5-hetero (1944/729-6). d, ⑥+4II (1943/1170-5). e, ⑧+3II (1945/657-8). f, ⑩+2II (1946/161-1). g, ⑫+1II (1946/264-4). h, ⑭ (1950/337-2). 4 a, b, Microphotographs of original 7II and a synthesized ⑭ (1950/337-2). a, *T. aestivoides*, 7II, after Kihara's (1924) photomicrograph.

Table 7 shows the fertilities of normal and RT-plants with induced or synthesized rings (one or more).

Discussion

Ring configurations in meiosis were first observed in *Oenothera* by Gates as early as 1908. But more than ten years had passed before the chromosomal basis and genetic significance of the phenomenon were

Table 7. Fertility of plants with pairs and rings

Material	Pollen fertility	Seed setting	
		Ears pollinated	Ears free or bagged ¹
Control			
<i>T. aegilopoides</i> 7II	99.17		83.33
<i>T. monococcum</i> 7II	98.30		87.17
④+5II	82.66		56.66
aT1	92.66		51.21
aT2	90.02		57.44
aT3	89.80		45.45
aT4	—		57.69
aT5	92.06		71.11
mT1	—		75.00
mT2	90.58		59.22
mean.....			
④+④+3II	80.58		46.48
④+④+④+1II	67.92		37.50
⑥+4II	76.30		51.72
⑥+④+2II	70.89		65.78
⑥+④+④	34.85	48.85	29.12
⑥+⑥+1II	51.10		19.35
⑧+3II	48.71		37.50
⑧+④+1II	40.24		28.57
⑧+⑥	37.38		{ 0
			{ f: 26.66
⑩+2II	40.11	32.82	{ 0
			{ f: 8.82
⑩+④	20.36	9.33	{ 1.58
			{ f: 6.79
⑫+1II	29.64	18.59	{ 0
			{ f: 28.18
⑭	12.55	13.72	{ 0
			{ f: 4.38

¹ f: free, all other bagged.

laid clear by Cleland (1922). Since then, an imposing amount of literature has accumulated dealing with this phenomenon, found also in a number of other genera, either in nature or in experiments following irradiation. The studies of Belling and Blakeslee (1926) in *Datura* showed that the occurrence of rings in meiosis is due to segmental interchanges or reciprocal translocations between non-homologous chromosomes. Many other investigations, published later, arrived at the same conclusion.

In Einkorn wheats, papers dealing with X-ray induced RT's were published by Katayama (1935), Smith (1936, 1939 and 1943), W. P. and M. G. Thompson (1937), Kihara (1942), Matsumura (1946) and the present author (1947, 1948, 1949 a and b, 1950 a and b).

RT's found in heterozygous condition in X_1 have usually configurations of ④, ④+④ or ⑥, but Smith (1939) obtained in addition larger rings, such as ⑥+④, ⑧ and ⑩. Some of the RT's used in my investigations were found as heterozygotes in X_1 , while some others were obtained in later generations. Most of the homozygotes were found recently. They were analyzed in rather laborious crossing experiments, and the segmental arrangements of several of them were ascertained (Tabs. 3 and 4). Fig. 5 shows the schema of segmental arrangements

in one of the RT-series in alphabetical order, from a to g.

Following the analysis, RT-chromosomes of known constitution were combined into larger rings by successive crossing experiments, carried out systematically according to the plan laid down in Fig. 2. At last,

Fig. 5. Schema showing the segmental arrangements of RT-chromosomes. (+ represents the original chromosome).

in 1950, the synthesis of every type of ring configuration was accomplished (Tabs. 1, 6 and 7). Fig. 6 shows the schema of segmental constitutions in one of the synthesized ⑭ in the cross combinations of Tab. 6, series B. It should be noticed that only two chromosomes of the ring, i.e. a and g, have the original constitution, while all remaining are interchanged.

Fig. 6. Schema showing a synthesized ⑭.

In the cross combinations of Tab. 6, series A, the crosses were so planned that the chromosomes of *T. monococcum* associate with those of *T. aegilopoides* in every ring. The female parents were heterozygotic for three RT's induced in *T. monococcum* and their embryosacs possessed one, two or all three of them, while the male parents were homozygotic for three RT's induced in *T. aegilopoides* and all pollen grains must have had all three together. Therefore,

$$\textcircled{14} = \frac{b \ a-c \ d-e \ f-g}{b-a \ c-d \ e-f \ g} = \frac{T. \ monococcum}{T. \ aegilopoides} \text{ or } monococcum \cdot aegilopoides\text{-complex heterozygote.}$$

In 4-chromosome rings, as well as in larger ones only the zigzag arrangement of the chromosomes with the following separation of

alternate chromosomes results in viable, normal gametes. The frequency of zigzag figures in a ring of four amounted to 82.69% on an average, ranging from 75.63 to 91.37% (Tab. 5). This frequency value represents the disjunctional coefficient which I have designated with the symbol d . The disjunctional coefficient should be in accord with the pollen fertility which I found to be a little higher (90.58% on an average). For the present, the value of d may be settled as about 85%, though it will vary in different RT-heterozygotes.

Generally speaking, the division of a ring is initiated by one of the kinetochores and the behavior of the neighbouring chromosomes, i.e. whether they move to the opposite poles or to the same pole, will be determined by the rate of repulsion between the homologous segments, as suggested by Gairdner and Darlington (1931), Kihara (1932) and Darlington (1937). The process will occur in succession in a larger ring, with the rate of repulsion represented by the disjunctional coefficient d .

From Fig. 7 it becomes evident that the number of all possible configurations will be obtained by the expansion of the binomial expression $(d + 1 - d)^r$ in which r is the number of RT-sets combined into a ring. Therefore the frequency of zigzags is determined by d^r . If more than two rings are present, the zigzag frequency is represented by the product of the individual frequencies obtained for every ring, i.e. $d^{r_1} \times d^{r_2} \dots = d^{r_1 + r_2 + \dots}$. Consequently, as functional gametes will result only from disjunctional figures, a general formula for the fertility (y) can be given as $y = kd^t$ (k is usually 1; t is the total number of RT-sets combined).

The pollen fertility given in Tab. 7 is represented graphically in Fig. 8. The observed curve of fertility degrees follows approximately the theoretical curve corresponding to $y = kd^t$, with $d = 85\%$, but is somewhat lower for the larger rings. This is probably due to the more frequent occurrence of irregularities in the division of larger rings. In a plant with ⑫ the % of complete zigzags amounted to 22.22% which was approximately in accord with the pollen fertility of 29.64% (Tabs. 5 and 7).

Fig. 7. Schema showing the division of ring-chromosomes, with the disjunctional coefficient $= d$.

In Fig. 9 the fertility curve for Einkorn is given which was obtained by Smith (1939). It is in very good accord with my results (Fig. 8). The same figure shows also the fertility curve for *Zea* (after Brink and Cooper/1932/and others). It corresponds to the theoretical curve with the value of d fixed at 50%.

Fig. 8. Graph showing pollen fertility given in Tab. 7.

In *Oenothera* the ring is usually arranged in a zigzag, so that $d = 100\%$. However, 10–30% non-disjunctions could be observed in any ring (Cleland 1924, 1926 and 1929). According to the data of Gates and Catcheside (1932) the fertility in one group of the species hybrids of *Oenothera* comes to about 80% and in another to about 40%, with a few exceptions (Fig. 10), and the low fertility in the latter group was explained by the mechanism of balanced lethals which should result in 50% sterility. Therefore the formula $y = kd^t$ is also applicable to *Oenothera*, if we fix the value of k at 0.8 or 0.4; d will be of course 100%. As to a few exceptions in which no mechanism of balanced lethals was found and yet low fertility was observed, it was attributed to a lack of harmony in the hybrids between plasma and nucleus.

The percentage of seed setting in my Einkorn experiments was somewhat lower than that of fertile pollen grains. Insufficient pollination is supposed to be the cause, as the flowering time of Einkorn

Fig. 9. Graph showing pollen fertility in *Zea* (A, data from Brink and Cooper/1932/ and others) and in Einkorn (B, data from Smith, 1939).

Fig. 10. Graph showing pollen fertility in *Oenothera* (data from Gates and Catchside, 1932).

wheats coincides in Kyoto with the rainy season.

In plants with ⑧+⑧, ⑩, ⑩+④, ⑫ or ⑭ the anthers were very hard to tear asunder and the ears, when bagged, set very few seeds or none at all. The unbagged ears or ears pollinated by hand produced some seeds (Tab. 7). For instance, the plants with ⑭ had a seed set of 13.72%, when pollinated by hand, which was in accord with the percentage of fertile pollen grains. In unbagged ears the seed set amounted to 4.38%. From these data, the frequency of spontaneous cross fertilization (λ) can be calculated as follows:

$$\lambda = \frac{\text{fertility in unbagged condition}}{\text{fertility at artificial pollination or pollen fertility}} \\ = \frac{4.38}{\text{ca. } 13} = \text{ca. } 33 \text{ (\%)}$$

In *Oenothera*, according to Cleland (1935, 1940), species with small rings are found in California, while in the east species with larger rings are predominant. From this distribution the conclusion was drawn that California is the home of *Oenothera*. It is very interesting in this connection that every type of ring obtainable from 10 chromosomes was also found in *Paeonia* species which occur in California (Stebbins and Ellerton 1939, Walter 1942).

I have succeeded in synthesizing in the Einkorn wheats every type of ring complex known in *Oenothera* by combining the basic RT's in successive crossing experiments. From my results the conclusion may be drawn that a number of basic RT's in *Oenothera* originated in Cali-

fornia in the course of the development of the genus, and the larger rings were synthesized in succession through manifold natural crosses during the migration to the east.

Summary

Reciprocal translocations (RT's) induced by X-ray treatments of dormant seeds of Einkorn wheats, *Triticum aegilopoides* and *T. monococcum*, were analyzed and their chromosome constitutions established.

In the attempts to combine the chromosomes into larger rings, successive crosses among the established RT-types have been carried out and all possible combinations of rings and pairs obtainable from the 14 Einkorn chromosomes were realized, resulting in a series of structural hybrids comparable with the well known situation in *Oenothera*. In one of the cross combinations, the crosses were so planned that the chromosomes of *T. monococcum* associate with those of *T. aegilopoides* in every ring. In this way was the ⑭-*monococcum* · *aegilopoides* complex heterozygote obtained.

Fertility relationships and the evolutionary processes of plants with ring complexes were discussed.

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