Spontaneous reciprocal translocations in cultivated form of Emmer wheat¹⁾

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ABSTRACT

Twenty-one F_1 hybrids among fourteen varieties or cultivars of cultivated form of Emmer wheat were studied with respect to chromosome pairing at MI of PMC's, and four chromosome types were determined according to the reciprocal translocations detected.

In relation to LD 222 type that was recognized as a standard, Ethiopicum type had a reciprocal translocation between 2A and 4A, and two translocations among three chromosomes, i.e. 4A-2A:2A-2B, were carried by Abyssinicum type. Liguliforme type had two different translocations, the one being between 7A and 5B, but the other unidentified.

1. INTRODUCTION

Reciprocal translocation or segmental interchange of chromosomes can be detected by a ring or a chain of chromosomes formed at the first meiotic metaphase in the heterozygote. There are a lot of spontaneous reciprocal translocations found in various plant species (Burnham 1956). *Oenothera* and *Rhoeo* are widely known because of the ring linking up all the chromosomes in the translocation heterozygote.

Reciprocal translocation may serve as a tool for cytogenetical researches. The artificially induced reciprocal translocations have been investigated most intensively in maize and followed by barley, rice and some others. In wheat Yamashita (1950) studied the induced reciprocal translocations in diploid wheat and succeeded in linking all fourteen chromosomes in a ring in the heterozygote for six different reciprocal translocations. Some earlier instances of the reciprocal translocation in Emmer wheat were reported by Hosono (1935), Smith (1947), Nishikawa (1962) and Dalal and Sadanaga (1965). Kawahara and Tanaka (1978) and Kawahara (1984) studied intraspecific structural differentiation of chromosomes, especially reciprocal translocations in wild tetraploid wheats. In hexaploid wheat, more studies have been reported (cf. Kawahara 1984).

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It is of a great importance to identify chromosomes involved in the reciprocal translocation, and it is desirable, if possible, to determine the break points. Among studies in wheat there are several reports, in which the monosomic series of common wheat has been used for identifying chromosomes involved in reciprocal translocations (cf. Kawahara 1984). Dalal and Sadanaga (1965) identified chromosomes 2A(II) and 3A involved in a reciprocal translocation in *T. carthlicum* by use of Chinese Spring monosomics. Telocentric chromosomes may be useful as the markers, Linde-Laursen and Larsen (1974) used doublemonotelodisomics to identify translocations in common wheat.

In this paper reported are four chromosome types found in cultivated Emmer wheat and identification of the chromosomes involved in the translocations.

2. MATERIALS AND METHODS

Following fourteen varieties or cultivars were used, which all belong to *Triticum turgidum* (L.) THELL.;

ssp. *dicoccum* (SCHRANK) THELL. var. *liguliforme*, var. *aureum*, cv. Khapli, cv. Vernal

ssp. *georgicum* (DEK. et MEN.) MK var. *georgicum*

ssp. *turgidum* conv. *durum* (DESF.) MK var. *reichenbachii*, var. *melanopus*, var. *africanum*, var. *ethiopicum*, var. *abys-sinicum*, var. *pyramidale*, cv. LD 222, *sphaerococcum* type mutant*

cov. *polonicum* (L.) MK var. *gracile*

Among these varieties or cultivars, twenty-one F₁'s were raised and studied with respect to chromosome pairing at the first meiotic metaphase. Aceto-carmin squash method was applied to PMC's fixed with Farmer's fluid.

3. RESULTS

1. Four chromosome types detected in cultivated Emmer wheat

Twenty-one different hybrids represented in Table 1 were studied with respect to chromosome pairing at MI of PMC's. In those hybrids involving LD 222 as one of parents and Vernal, *reichenbachii*, *sp* type mutant or *polo-nicum* as the other, complete pairing of 14 bivalents was observed in almost all PMC's. It was the same with the hybrid between Vernal and *georgicum*. There was, in addition to 13 bivalents, one trivalent having two telocentrics, one associated with either end of a complete chromosome in 96% of PMC's in LD 222 × *melanopus* hybrid. These observations clearly indicate that LD

*Schmidt and Johnson (1963).

Table 1. Chromosome pairing at MI of PMC's in twenty-one different hybrids in cultivated form of Emmer wheat

Cross combination	Pairing type	Frequency (%)
LD 222×Vernal	14''	84.5
" × <i>reichenbachii</i>	14''	100.0
" × <i>polonicum</i>	14''	98.6
" × <i>sp</i> like mutant	14''	90.3
" × <i>melanopus</i>	(t+t)1''' + 13''	96.0
Vernal× <i>georgicum</i>	14''	100.0
<i>liguliforme</i> × <i>aureum</i>	14''	90.4
<i>ethiopicum</i> ×LD 222	1''' + 12''	95.7
" × <i>africanum</i>	1''' + 12''	77.5
" × <i>abyssinicum</i>	1''' + 12''	98.4
<i>liguliforme</i> ×LD 222	1''' + 12''	100.0*
" × <i>georgicum</i>	1''' + 12''	100.0*
<i>aureum</i> ×LD 222	1''' + 12''	63.8
	2''' + 10''	29.5
<i>melanopus</i> × <i>liguliforme</i>	(t+t)3''' + 12''	76.1
	(t+t)3''' + 1''' + 10''	17.4
<i>abyssinicum</i> ×LD 222	1''' + 11''	71.4
" × Khapli	1''' + 11''	75.7
" × <i>pyramidale</i>	1''' + 11''	100.0
" × <i>georgicum</i>	1''' + 11''	100.0*
" × <i>melanopus</i>	1''' + (t+t)1''' + 10''	76.4
" × <i>liguliforme</i>	1''' + 1''' + 9''	90.0
" × <i>aureum</i>	1''' + 1''' + 9''	79.5

* Only a few PMC's checked.

222 and others involved in these hybrids carry the same chromosome type. There was one more hybrid between *liguliforme* and *aureum* that formed 14 bivalents in 90.4% of PMC's with a few exceptions having a quadrivalent.

Three hybrids having *ethiopicum* as a female parent formed 1''' + 12'' in most of PMC's. The same pairing was confirmed in the respective hybrids of *liguliforme* pollinated with either LD 222 and *georgicum*. While in the hybrid between *aureum* and LD 222 two quadrivalents were observed in about 30% of PMC's in addition to those (63.8%) of 1''' + 12'' that was observed in F₁ (*liguliforme*×LD 222). The hybrid between *melanopus* and *liguliforme* formed a quinquevalent marked with two telocentrics, one associated with either end of a chain of three complete chromosomes. This indicates that chromosome 5B takes part in a translocation of *Liguliforme* type, because *melanopus* carries 15 pairs of chromosomes (Tsunewaki 1963), of which two pairs are known to be the long and short arm telocentrics of chromosome 5B

Fig. 1. Microphotographs showing chromosome pairing in PMC's. A: *abyssinicum* $\times$ LD 222 F_1 (1''''''+11''), B: *abyssinicum* $\times$ *liguliforme* F_1 (1''''''+1''''+9''), C: 7A telocentric F_1 of *liguliforme* ((t+t)3'''''+12''), D—F: *abyssinicum* F_1 telocentric for 2A (D) ((t+t)5'''''+11''), 4A (E) (t3'''''+t2'''+11'') and 2B (F) (t4'''''+t1'''+11'')

(Nishikawa unpublished). Furthermore, it formed another chain of four in some 20% of PMC's in addition.

Seven *abyssinicum* hybrids formed a sexivalent (Fig. 1-A) in at least 70% of PMC's. In the rest the sexivalent dissociated to form two trivalents, one quadrivalent and one bivalent or one quinequevalent and one univalent. It is evident from these observations that there are two translocations involving three chromosomes that differentiate *abyssinicum* from others. 5B telocentrics from *melanopus* formed a heteromorphic trivaleat. Two *abyssinicum* hybrids with either *liguliforme* and *aureum* formed a quadrivalent in addition to a sexivalent (Fig. 1-B) in almost all PMC's checked.

Summarizing the pairing behavior shown in Table 1, four chromosome types can be distinguished (Table 2). LD 222 type seems to be primitive (Nishikawa 1967) and is the most prevalent as evident in this study. So it is reasonable to assume that LD 222 type is a standard type. Ethiopicum type on one hand and *liguliforme* and *aureum* on the other, though different from LD 222 type by one reciprocal translocation, showed different pairing behavior to *abyssinicum*. Then, it is considered that *ethiopicum* has the reciprocal translocation common to one of the two detected in *abyssinicum*,

Table 2. Four chromosome types deduced from pairing analysis in the hybrids of cultivated form of Emmer wheat

LD 222 type	Ethiopicum type	Abyssinicum type	Liguliforme type
LD 222, Vernal, Khapli, <i>georgicum</i> , <i>reichenbachii</i> , <i>africanum</i> , <i>melanopus</i> , <i>sp</i> like mutant, <i>pyramidale</i> , <i>polonicum</i>	<i>ethiopicum</i>	<i>abyssinicum</i>	<i>liguliforme</i> <i>aureum</i>

while *liguliforme* and *aureum* have one reciprocal translocation different from those of *abyssinicum*. Further, *liguliforme* and *aureum*, though formed a rare quadrivalent in their hybrid, seem to be very similar, if not completely the same, in the chromosome type.

2. Identification of chromosomes involved in the reciprocal translocations

The hybrids telosomic or monosomic for the respective chromosomes were raised. These hybrids are denoted as 1A through 7B in Table 3 according to the chromosome in such condition.

a) *Ethiopicum* type

Chromosome pairing observed in the hybrids of LD 222 telosomic lines with *ethiopicum* is represented in Table 3. Lines 1A, 3A and 5A through 7B, which were doubletelotrisomic showed pairing type $1''' + (t+t)1''' + 11''$ in most of PMC's checked. These lines are non-critical. One trivalent and one univalent, instead of a quadrivalent, were formed in some of these lines, especially in 7A in about 20% of PMC's. One telocentric chromosome, probably of short arm, occasionally failed to associate with its homologue and resulted in a heteromorphic bivalent and a univalent in lines 1A, 5A, 6A, 2B and 4B. Line 2A was monotelodisomic, having the long arm telocentric of chromosome 2A. It formed a heteromorphic quadrivalent with the telocentric associated with one end of a chain of three complete chromosomes in 70% of PMC's. The remaining PMC's had a telocentric univalent and a chain of three completes. Line 4A, which was doubletelotrisomic, formed a quinquevalent marked with two telocentrics in 81% of PMC's. One or two telocentrics were rarely dissociated from the quinquevalent as univalents. From these observations, it is quite evident that lines 2A and 4A are the critical lines and *Ethiopicum* type of reciprocal translocation is between chromosomes 2A and 4A.

b) *Abyssinicum* type

Two series of aneuploid hybrid lines were raised; one is a series involving LD 222 telosomic lines and the other Chinese Spring monosomic lines. In telosomic hybrid lines which were doubletelotrisomic, non-critical pairing

Table 3. Percentages of PMC's having the indicated pairing types in the respective hybrids of LD 222 telosomic series and Chinese Spring monosomic series crossed with *ethiopicum*, *abyssinicum* and *liguliforme*

Pairing type	Telosomic or monosomic for chromosome													
	1A	2A	3A	4A	5A	6A	7A	1B	2B	3B	4B	5B	6B	7B
LD 222 telosomic $\times$ <i>ethiopicum</i>														
(t+t)3''''+12''	0	0	0	81.0	0	0	0	0	0	0	0	0	0	0
t3''''+12''	0	72.5	0	0	0	0	0	0	0	0	0	0	0	0
1''''+(t+t)1'''+11''	82.5	0	98.1	0	90.0	72.0	77.5	100.0*	81.4	92.0	92.0	100.0	100.0*	83.3
LD 222 telosomic $\times$ <i>abyssinicum</i>														
(t+t)5''''''+11''	0	71.0	0	81.0	0	0	0	0	66.3	0	0	0	0	0
1''''''+(t+t)1'''+10''	80.0	0	96.0	0	85.5	86.5	69.2	75.0	0	90.1	98.2	70.2	74.6	84.6
CS monosomic $\times$ <i>abyssinicum</i>														
1'''''+11''+7'	2.7	49.8	2.7	43.5	3.3	4.3	4.7	2.5	41.8	6.1	5.8	4.7	2.8	2.7
1'''''+10''+8'	62.6	0	69.2	0	67.9	68.3	71.8	77.4	0	50.6	77.7	70.0	79.8	79.3
LD 222 telosomic $\times$ <i>liguliforme</i>														
(t+t)3'''''+12''	0	0	0	0	0	0	75.9	0	—	0	0	88.0	0	0
1'''''+(t+t)1'''+11''	96.9	0	97.1	91.8	0	97.0	0	97.2	—	91.2	94.1	0	95.9	94.9
1'''''+(t+t)1'''+11''+1'	0	0	0	0	63.8	0	0	0	—	0	0	0	0	0
1'''''+t1''+11''	0	85.7	0	0	0	0	0	0	—	0	0	0	0	0
CS monosomic $\times$ <i>liguliforme</i>														
1''''+12''+7'	4.9	5.1	1.8	3.6	1.0	4.1	36.7	2.1	8.1	9.0	6.7	—	—	—
1''''+11''+8'	68.7	52.2	80.9	60.5	74.8	60.6	9.6	62.3	75.6	72.9	66.6	—	—	—

* Only a few PMC's checked.

type, $1'''' + (t+t)1''' + 10''$, was confirmed in all but lines 2A, 4A and 2B. Among the variant pairing types in these lines, though not listed in Table 3, the one having one telocentric as a univalent was the most common and remarkable (ca. 21%) in line 1B. Another variant type, especially noticeable (ca. 25%) in 7A, was occurrence of two univalents of complete chromosomes. While in lines 2A, 4A and 2B, the critical pairing type, $(t+t)5'''' + 11''$ (Fig. 1-D), was observed with the frequencies of 71.0%, 81.0%, 66.3%, respectively. Most of the variant pairing types were dissociation of the telocentric marked septivalent to the component parts, which will be considered later.

In the monosomic hybrid lines, the critical pairing type, $1'''' + 11'' + 7'$, was confirmed, as expected, in lines 2A, 4A and 2B, with moderate frequencies, but rarely in the other lines which showed mostly non-critical pairing type, $1'''' + 10'' + 8'$. In every lines, either critical and non-critical, some variant pairing types occurred with considerable frequencies; for example dissociation of a sexivalent into $1'''' + 1''$ or $2'''$ in non-critical lines and dissociation of a quinquevalent into $1'''' + 1'$ or $1''' + 1''$ in the critical lines. Consequently it is concluded without doubt that chromosomes 2A, 4A and 2B are involved in the two reciprocal translocations of Abyssinicum type.

As shown in the previous paragraph, 2A-4A translocation was detected in Ethiopicum type. Accordingly, it seems reasonable to assume that Abyssinicum type translocations could result from an additional reciprocal translocation between 2A and 2B or between 4A and 2B, that occurred in Ethiopicum type. The alternative hypothesis that one translocation comes from *abyssinicum* and the other from LD 222 can be excluded based on the pairing behavior in F_1 's listed in Table 1. In the telosomic and monosomic hybrid lines for 2A, 4A and 2B, a multivalent failed to remain fully associated and separated to component parts with the relative frequencies shown in Table 4. These variant pairing types would provide some clues as to which additional translocation, 2A-2B or 4A-2B could occur. Fig. 2 shows the assumed pachytene configuration in the heterozygote for Abyssinicum type translocation. There are six arms where dissociation due to desynapsis or precocious chiasma terminalization could occur (Fig. 2 a-f). Generally speaking, dissociation is little likely to occur in the non-translocated arms (e and f), and probably so in the present case because of metacentric nature of all three chromosomes involved. In Table 4 it is remarkable that pairing types, $t5'''' + 1'$ and $t4'''' + t1''$ in telosomic hybrid 2A and $1'''' + 1'$ in monosomic hybrid 2A occurred with very low frequencies. If the above assumption of rarer dissociation at arms e and f were true, chromosome 2A should be present at position C. Considerably high occurrence of $t3'''' + t2'''$ (Fig. 1-E) and $1'''' + 1''$ found in both hybrid lines of 2A are best explained by the assumption mentioned above. If position C were occupied alternatively by chromosome 4A, dissociation at e and f should occur with the higher frequencies and as high as at a and b in mono-

Table 4. Percentages of PMC's having the indicated pairing types of the partially dissociated multivalent in the hybrids of LD 222 telosomics and Chinese Spring monosomics crossed with *abyssinicum*

Pairing type	Telosomic or monosomic for chromosome		
	2A	4A	2B
Telosomic hybrid			
t5'''''+t'	5.5	37.4	19.3
t4'''''+t1''	8.3	16.8	38.9
t3'''''+t2'''	75.2	33.2	38.6
others*	11.0	12.6	3.3
Monosomic hybrid			
1''''+1'	4.0	47.9	43.2
1''' + 1''	96.0	52.1	56.8

* The types not distinguishable one from the other.

Fig. 2. Assumed pachytene configuration in the heterozygote for Abyssinicum chromosome type.

somic hybrid in particular. This is not consistent with the above assumption. Then, locating chromosomes 2A, 4A and 2B at positions C, A and B respectively, the higher rate of dissociation at a and/or b would be estimated from the highest occurrence of t3'''''+t2''' in telosomic hybrid 2A. Comparing the frequencies of t5'''''+t' and t4'''''+t1'' (Fig. 1-F) between lines 4A and 2B the dissociation rate at a seems to be twice as high as at b, which is not inconsistent with the above assumptions. Considering the frequencies of t3'''''+t2''' in these three telosomic hybrids, the dissociation rates at c and d are roughly estimated as nearly half as those at a and b. If it is the case, however, t5'''''+t' should occur with much more frequency. Therefore, though it is not valid to estimate from data now available the dissociation rate at each of six arms, three chromosomes 2A, 4A and 2B can be located at position C, A and B in Fig. 2, respectively. Accordingly, *abyssinicum*'s additional reciprocal translocation that occurred in Ethiopicum chromosome type can be concluded to be between the non-translocated arm of chromosome 2A and

chromosome 2B.

c) *Liguliforme* type

As in the case of Abyssinicum type two aneuploid hybrid series, though more or less incomplete, were raised. Telosomic hybrid line 2A was monotelodisomic and the others were doubletelotrisomic, with the exception of line 5A that had an unidentified extra chromosome. As evident from Table 3, $(t+t)3''' + 12''$, a typical critical pairing type was confirmed in telosomic hybrid lines 7A and 5B, but not found in the other lines. Dissociation of $(t+t)3'''$ into $t2''' + t1''$ occurred in about 20% of PMC's in line 7A. On the other hand, non-critical pairing type occurred in the other lines with high frequencies. The most common variant type of pairing was such that the telocentric failed to associate and occurred as a univalent in those lines. The critical pairing type, $1''' + 12'' + 7'$, was detected more or less in all the monosomic hybrid lines checked, but with the highest frequency in line 7A. Then, 7A seems to be involved in this type of translocation. However, one of non-critical pairing types, $13'' + 8'$, was found in about 40% of PMC's even in 7A, but it is considered to be the result from dissociation of the trivalent into bivalent and univalent. $1''' + 11'' + 8'$, non-critical pairing type was found again in all the lines checked, but with the lowest frequency in line 7A. As evident in the foregoing section, Liguliforme type translocation involves chromosome 5B as a partner, and all the evidences so far available indicate that chromosomes 7A and 5B are involved in Liguliforme type translocation. One of the features of pairing type in those hybrids involving either *liguliforme* and *aureum* is that two quadrivalents occurred simultaneously in some 20% or 30% of PMC's. Based on data from Chinese Spring-*liguliforme* hybrid it is estimated that the quadrivalent composed of 7A-5B translocation occurs alone in about 80% of PMC's and the rare quadrivalent of unknown chromosomes alone in a few percent of them. It should be noticed that the pairing type, $1''' + 1''' + 10'' + 7'$, that might be a critical pairing type was found in 29.6% of PMC's in line 2A. Then, the assumption that a rare quadrivalent involves chromosome 2A as one of the partners may not be excluded.

4. DISCUSSION

In the present study, varieties and cultivars of cultivated Emmer wheat could be grouped into four chromosome types according to the reciprocal translocations detected at MI as a ring or a chain of multivalent. Besides LD 222 type that is considered as a standard type, identifying Ethiopicum type as 2A-4A reciprocal translocation, Abyssinicum type as 4A-2A:2A-2B and Liguliforme type as 7A-5B is consistent with the pairing behavior observed in the intergroup hybrids represented in Table 1. Kawahara (1984) presented in his doctor thesis the review of papers that reported translocations in *Triticum* and *Aegilops*. In tetraploid wheat only one that reported by Dalal and

Sadanaga (1965) showed chromosomes involved, i.e. *carthlicum* had a reciprocal translocation between 2A(II) and 3A. Kawahara himself identified five translocations in wild Emmer, and showed the genomes to which the translocated chromosomes belong; three were between chromosomes of genome B, one between those of genome A and another between those of genome A and B. According to Kawahara's summarization, chromosomes of genome B were involved most often in reciprocal translocations in hexaploid wheat, 7B being the highest in the whole and 4A the highest among chromosomes of genome A. In cultivated form of Emmer wheat, chromosomes 2A, 3A, 4A, 7A, 2B and 5B were so far proved to be involved in four different translocations, only 2A in three cases. Therefore, A genome chromosomes were involved six times and B genome ones two times in cultivated form of Emmer wheat, that is rather in contrast to hexaploid wheat. However, chromosome identification of Kawahara's six chromosome types still remains to be worked out before further considerations.

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