Studies on the Factors Controlling the Formation of Unreduced Gametes in Hybrids between Tetraploid Emmer Wheats and *Aegilops squarrosa* L.¹⁾

Kensuke FUKUDA²⁾ and Sadao SAKAMOTO

*Plant Germ-plasm Institute, Faculty of Agriculture, Kyoto University,
Mozume, Muko, Kyoto, 617 Japan*

The formation of the unreduced gametes must have played a major role on the formation of bread wheat. The authors reported its cytological process in the F₁ hybrids between tetraploid emmer wheats and *Aegilops squarrosa*. The present investigation was carried out to clarify the factors affecting the formation of unreduced gametes in these hybrids. Data of crossability as well as fertility were investigated and analyzed in detail. Unreduced gametes were formed with relatively high frequency in the following cases: (1) when *Triticum carthlicum* was used as female and *Ae. squarrosa* ssp. *strangulata* or var. *meyeri* as male parent, (2) when spikes headed relatively later, (3) in spikes of secondary or subsequent tillers. The promotion of unreduced gamete formation in F₁ hybrids between *T. carthlicum* and *Ae. squarrosa* ssp. *strangulata* or var. *meyeri* is genetically controlled.

KEY WORDS: *Triticum carthlicum*, *Aegilops squarrosa* ssp. *strangulata*, var. *meyeri*, unreduced gamete, crossability, pollen fertility, seed fertility.

Introduction

Bread wheat (*Triticum aestivum* L.) is a successful allohexaploid with AABBDD genomes, which has been derived as an amphiploid between tetraploid emmer wheat (AABB) and *Aegilops squarrosa* L. (DD) (KIHARA, 1944; MCFADDEN and SEARS, 1944). Since this had been revealed, many attempts have been made to synthesize bread wheat artificially using some varieties of tetraploid emmer wheat and *Ae. squarrosa* in view of genetic research and expanding breeding potentiality (KIHARA, 1949 *etc.*). Using the accessions collected by Kyoto University Scientific Expedition to the Karakoram and Hindukush in 1955, it was suggested that *T. carthlicum* NEVSKI, one of tetraploid emmer wheats, and *Ae. squarrosa* ssp. *strangulata* EIG or var. *meyeri* GRISEB. had some genetic factors which induced high fertility in their triploid hybrids (KIHARA *et al.*, 1965). These hybrids formed unreduced gametes with high frequency. Although this has been also suggested by other authors, no detailed investigations were reported so far. The present authors intended to clarify the mechanisms underlying the formation of unreduced gametes in detail. Firstly, its cytological process was minutely investigated, and the results were already reported (FUKUDA and SAKAMOTO, 1992). Secondly, the factors involved with it were analyzed by means of comparing the frequencies of the formation of unreduced gametes under various conditions. In this article, results of the latter investigations are described.

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¹⁾ Contribution No.60 from Plant Germ-plasm Institute, Faculty of Agriculture, Kyoto University, Kyoto, Japan

²⁾ Present address: Plant Bioengineering Research Laboratories, Sapporo Breweries Ltd., 37-1 Kizaki, Nitta, Gunma, 370-03 Japan

Materials and Methods

The materials used in the present investigation are indicated in Table 1. Nine accessions of tetraploid emmer wheat and five of *Ae. squarrosa*, all of which were maintained at Plant Germ-plasm Institute, Faculty of Agriculture, Kyoto University, were used. The former were used as female parent and the latter as male parent to produce F₁ hybrids. Crossings in reciprocal directions were also made in two combinations. F₁ seeds obtained were sown and root-tips were collected to check their somatic chromosome numbers. Thereafter, all the seedlings were individually planted in pots in an unheated greenhouse. Plants identified as hybrid were used for the further investigations.

The factors controlling the formation of unreduced gametes in the F₁ hybrids were analyzed on the basis of two kinds of data. One is the crossability between the parents and the other is the frequency of the formation of unreduced gametes.

Crossability was estimated from the following three kinds of values;

- (1) seed set rate (%): number of seeds obtained per number of florets pollinated.
- (2) germination rate (%): number of seedlings per number of seeds sown.
- (3) maturing rate (%): number of plants headed per number of seedlings.

Frequency of the formation of male and female unreduced gametes was estimated by pollen

Table 1. The materials used in the present investigation

Species	Accession No. (KU)	Abbreviation
(A) Tetraploid emmer wheat (2n=4x=28; AABB genomes)		
<i>Triticum dicoccoides</i> KÖRN.		
var. <i>spontaneonigrum</i> FLAKSB.	109	DIS
<i>Triticum dicoccum</i> SCHÜBL.		
var. <i>rufum</i> KÖRN. (Vernal)	124	DIM
<i>Triticum durum</i> DESF.		
var. <i>reichenbachii</i> KÖRN.	125	DUR1
var. <i>murciense</i> KÖRN. (Gulab)	134	DUR2
var. <i>obscurum</i> KÖRN. (Stewart)	136	DUR3
<i>Triticum orientale</i> PERC.		
var. <i>insigne</i> PERC.	137	ORI
<i>Triticum carthlicum</i> NEVSKI		
var. <i>stramineum</i> ZHUK.	138	CAR1
var. <i>fuliginosum</i> ZHUK.	139-1	CAR2
var. <i>fuliginosum</i> ZHUK. (Black Persian)	139-2	CAR3
(B) <i>Aegilops squarrosa</i> L. (2n=2x=14; DD genome)		
var. <i>typica</i> L.	20-1	TYP1
var. <i>typica</i> L.	20-2	TYP2
var. <i>typica</i> L.	20-3	TYP3
ssp. <i>strangulata</i> EIG	20-9	STR
var. <i>meyeri</i> GRISEB.	20-10	MEY

and seed fertility, respectively. They were assessed in the following ways.

Pollen fertility was represented by the percentage of number of fertile pollen grains per total number of pollen grains observed. Pollen grains were stained in aceto-carmin containing glycerin (1% aceto-carmin, 45% acetic acid, and glycerin to the ratio 1:3:3) in order to observe nuclei of pollen grains. After one month of staining, they were microscopically examined and those showing the following four characters were regarded as fertile grains;

- (1) having 3 morphologically normal nuclei in each grain,
- (2) being filled with starch granules and well-stained,
- (3) having single normal germ pore,
- (4) showing normal shape which was observed in the parental accessions.

Seed fertility was represented by the percentage of number of seeds per number of florets. Florets at least having both lemma and palea were taken into account because the size and morphology of the florets of the F_1 plants varied so much that strict distinction between abortive and normal ones was impossible. Seeds on the F_1 plants were obtained by self- and open-pollination, and they were independently calculated.

Data of these fertilities were arranged and considered in the following three ways;

- (1) variation among F_1 hybrids of various cross combinations,
- (2) variation among periods within heading time,
- (3) variation among tillers and florets.

Heading time was divided into periods of ten days, so that each month had three periods: I, II and III, although the last period of May contained 11 days. Therefore, data of pollen fertility were obtained in nine periods, from the I of April to the III of June, and those of seed fertility from ten periods, adding the I of July to those described above. Fertility of the parental accessions was also observed as controls.

Results

(A) Production of the F_1 hybrids and crossability of their parents

Forty-seven cross combinations of hybridization were intended using nine accessions of tetraploid emmer wheat and five of *Ae. squarrosa*. However, only 38 crosses could be made because of time lag on the flowering time among them.

Seed set rate varied from 0.0% in three crosses involved with TYP3 to 57.1% in one cross, STR/DIM, and the average was 24.9% (Table 2). As for female parents, seed set rate was low when DUR3 or ORI were used (10.8% and 10.0%, respectively). As for male parents, crosses involved with STR or MEY showed high values (33.7% and 44.4%, respectively). Those involved with TYP3 set few seeds (6.8%). Crosses of reciprocal directions, TYP1 or STR / DIM, successfully set seeds (50.0% and 57.1%, respectively).

Germination rate of the F_1 hybrids varied from 0.0% in seven hybrids to 100.0% in three hybrids, and the average was 43.4% (Table 3). As for female parents, hybrids involved with DIS, DUR1, or CAR1 showed high values (66.3%, 78.3% and 76.3%, respectively), while those with DIM showed a low value (13.3%). As for male parents, hybrids involved with TYP1 or TYP2 showed relatively low values. Any seeds obtained from the crosses in reciprocal directions did not germinate.

Table 2. Seed set rate (%) of the crosses between tetraploid emmer wheats and *Ae. squarrosa*

Female parent	Male parent						Average
	TYP1	TYP2	TYP3	STR	MEY	DIM	
DIS	—	16.3	15.8	40.3	—	—	24.1
DIM	29.6	10.4	—	44.9	—	—	28.3
DUR1	25.8	1.9	0.0	38.8	54.3	—	24.2
DUR2	7.1	16.3	0.0	43.3	36.8	—	20.7
DUR3	16.7	—	—	4.9	—	—	10.8
ORI	6.7	1.1	0.0	16.7	25.7	—	10.0
CAR1	16.0	50.0	12.5	49.6	54.2	—	36.5
CAR2	13.6	37.0	12.5	33.6	51.1	—	29.6
CAR3	8.5	16.7	—	31.6	—	—	18.9
TYP1	—	—	—	—	—	50.0	50.0
STR	—	—	—	—	—	57.1	57.1
Average	15.5	18.7	6.8	33.7	44.4	53.6	24.9

Table 3. Germination rate (%) of the seeds obtained from the crosses between tetraploid emmer wheats and *Ae. squarrosa*

Female parent	Male parent						Average
	TYP1	TYP2	TYP3	STR	MEY	DIM	
DIS	—	47.1	100.0	51.7	—	—	66.3
DIM	23.3	0.0	—	16.7	—	—	13.3
DUR1	63.3	100.0	—	76.7	73.3	—	78.3
DUR2	16.7	0.0	—	83.3	13.3	—	28.3
DUR3	50.0	—	—	42.9	—	—	46.5
ORI	0.0	0.0	—	86.7	50.0	—	34.2
CAR1	63.3	83.3	100.0	73.3	61.5	—	76.3
CAR2	12.0	50.0	0.0	46.7	54.2	—	32.6
CAR3	33.3	25.0	—	20.0	—	—	26.1
TYP1	—	—	—	—	—	0.0	0.0
STR	—	—	—	—	—	0.0	0.0
Average	32.7	38.2	66.7	55.3	50.5	0.0	43.4

Maturing rate of the hybrids varied from 0.0% to 100.0%, and the average was 49.3% (Table 4). Plants of 18 hybrids produced at least one spike. As for female parents, hybrids involved with DIS or ORI showed high values (91.4% and 74.0%, respectively), while those with DUR3 or CAR3 showed low values (22.2% and 27.8%, respectively). As for male parents, hybrids involved with STR showed high value (81.4%).

Vigor as well as morphological characteristics within each hybrid were uniform as expected. Hybrids were more vigorous than the others when DIS was used as female parent or

Table 4. Maturing rate (%) of the F₁ hybrids

Female parent	Male parent					Average
	TYP1	TYP2	TYP3	STR	MEY	
DIS	—	87.5	100.0	86.7	—	91.4
DIM	42.9	—	—	40.0	—	41.5
DUR1	0.0	0.0	—	87.0	63.6	37.7
DUR2	0.0	—	—	88.0	75.0	54.3
DUR3	0.0	—	—	66.7	—	22.2
ORI	—	—	—	92.3	55.6	74.0
CAR1	78.9	0.0	0.0	95.5	68.8	48.6
CAR2	0.0	0.0	—	92.9	76.9	42.5
CAR3	0.0	0.0	—	83.3	—	27.8
Average	17.4	17.5	50.0	81.4	68.0	49.3

Table 5. Grade of the crossability between the parents and of the vigor of the F₁ hybrids

Female parent	Male parent				
	TYP1	TYP2	TYP3	STR	MEY
DIS	—	V	V	V	—
DIM	IV	I	—	V	—
DUR1	II	II	0	IVd	IVd
DUR2	III	I	0	V	V
DUR3	III	—	—	IVd	—
ORI	I	I	0	Vd	IVd
CAR1	IV	IIIId	IIIId	V	V
CAR2	I	IIIId	I	V	V
CAR3	III	IIIId	—	V	—

0: No F₁ seeds obtained.

I: No seeds germinated.

II: Plants died only with one leaf expanded.

III: Plants died without spikes.

IV: Spikes headed but weak.

V: Spikes headed and vigorous.

d: Plants showed dwarfness.

when STR or MEY was used as male parent (Table 5). All the plants of nine hybrids showed characteristic dwarfness. These hybrids with dwarfness were classified into the following three types on the basis of their viability;

- (1) no spikes emerged: CAR1/TYP2, CAR1/TYP3, CAR2/TYP2 or CAR3/TYP2,
- (2) spikes emerged with many tillers: ORI/STR,
- (3) spikes emerged with fewer tillers: the remaining hybrids.

(B) Pollen fertility

(a) Variation among the F₁ hybrids

Data were obtained from 12 hybrids (Table 6). Overall average of the fertility of each hybrid varied from 0.2% in DUR2/MEY to 77.9% in CAR2/STR and the average was 45.4%. Five hybrids, DIS/TYP3, CAR1/STR, CAR1/MEY, CAR2/STR and CAR3/STR showed high values over 30.0%. Except for DIS/TYP3, they were derived from the crosses between *T. carthlicum* (CAR1, CAR2, and CAR3) and *Ae. squarrosa* ssp. *strangulata* (STR) or var. *meyeri* (MEY). Four hybrids, DIS/TYP2, DUR1/MEY, DUR2/STR and DUR2/MEY showed low values below 10.0%. Except for DIS/TYP2, their female parents were *T. durum* (DUR1 and DUR2, respectively).

Average of the fertility of whole hybrids in each heading period varied from 0.1% in the II and III of April to 55.2% in the II of June. Except for three hybrids, DIS/TYP3, DIM/STR, and CAR1/STR, all the hybrids examined showed the highest values at their latest heading periods. According to the highest value in each hybrid, the hybrids are roughly classified into the following three classes;

- (1) low values (at most 11.7%): DIS/TYP2, DUR1/MEY, DUR2/STR, and DUR2/MEY,
- (2) Intermediate values: DIS/TYP3, DIS/STR, and DIM/STR,
- (3) high values (more than 60.8%): CAR1/STR, CAR1/MEY, CAR2/STR, CAR2/MEY, and CAR3/STR.

Hybrids of the third class were all derived from the crosses between *T. carthlicum* and *Ae. squarrosa* ssp. *strangulata* or var. *meyeri*. Especially, 94.2% of CAR2/STR in the II of June was extremely high.

Table 6. Pollen fertility (%) of the F₁ hybrids

Cross combination	Heading period									Overall average ¹⁾
	April			May			June			
	I	II	III	I	II	III	I	II	III	
DIS/TYP2	—	—	—	1.0	4.3	0.7	<u>11.7</u>	—	—	4.0
DIS/TYP3	—	—	—	<u>52.6</u>	14.7	25.8	34.6	—	—	38.9
DIS/STR	—	—	—	0.0	<u>21.6</u>	—	—	—	—	14.7
DIM/STR	—	—	—	—	<u>37.2</u>	36.7	—	8.4	6.2	25.6
DUR1/MEY	—	—	—	—	—	—	—	—	1.5	1.5
DUR2/STR	0.2	0.1	0.0	0.2	2.6	<u>8.1</u>	—	—	—	0.6
DUR2/MEY	—	0.0	0.1	—	0.1	0.1	0.3	<u>1.9</u>	—	0.2
CAR1/STR	—	—	—	<u>60.8</u>	42.6	33.3	43.4	—	—	36.0
CAR1/MEY	—	—	—	1.2	9.3	2.0	44.3	<u>67.6</u>	—	41.2
CAR2/STR	—	—	—	5.2	3.6	82.1	93.5	<u>94.2</u>	—	77.9
CAR2/MEY	—	—	—	0.0	1.2	0.1	1.8	<u>74.9</u>	—	16.1
CAR3/STR	—	—	—	15.8	35.0	—	15.8	<u>84.1</u>	—	33.4
Average	0.2	0.1	0.1	15.2	15.7	21.0	30.7	<u>55.2</u>	3.9	45.4 ²⁾

Underlined figures indicate the highest value in each F₁ hybrid.

¹⁾Percent of total number of fertile pollen grains per total number of pollen grains observed

²⁾Average of the overall averages

Dehiscence of the anthers was observed in six hybrids, DIS/TYP3, DIM/STR, CAR1/STR, CAR1/MEY, CAR2/STR, and CAR3/STR, all of which showed relatively high values.

(b) Variation within an individual

(i) Among tillers

Data are summarized in Table 7. On the basis of the tillers in which the highest value was observed within each hybrid, hybrids are classified into the following two types;

- (1) main culm or primary tillers: DIS/TYP3, DIM/STR, CAR1/STR, and CAR3/STR,
- (2) secondary or subsequent tillers: DIS/TYP2, DIS/STR, DUR2/STR, DUR2/MEY, CAR1/MEY, CAR2/STR, and CAR2/MEY.

(ii) Among florets

All the anthers of whole florets within a spike of CAR1/STR headed on May 26th were sampled and pollen fertility of every floret was observed (Table 8). Forty-five florets of 14 spikelets flowered. In some spikelets, even the 4th florets flowered. Values of fertility widely varied from 0.6% (the 2nd floret of the 6th spikelet from the top) to 69.7% (the 3rd of the 5th), and the overall average was 33.9%.

(c) Pollen fertility of the parental accessions

Samples were collected in the middle of May. Fertility was higher in every accession than 90.0% and the average was 93.7%.

(C) Seed fertility

(a) Variation among the F_1 hybrids

Most of the seeds produced on the F_1 plants were normal and plump.

Table 7. Pollen fertility (%) of the different orders of tillers in the F_1 hybrids

Cross combination	Order of tillers ¹⁾				
	0	I	II	III	U
DIS/TYP2	4.4	3.2	<u>6.4</u>	—	—
DIS/TYP3	<u>69.9</u>	42.7	34.9	—	—
DIS/STR	—	—	<u>17.8</u>	10.3	—
DIM/STR	<u>39.3</u>	28.4	19.3	1.9	—
DUR2/STR	—	0.4	<u>4.4</u>	—	—
DUR2/MEY	0.0	0.0	0.1	<u>0.6</u>	—
CAR1/STR	12.9	<u>53.9</u>	45.8	—	34.0
CAR1/MEY	7.5	26.4	30.4	<u>78.6</u>	42.7
CAR2/STR	5.2	24.5	<u>92.3</u>	—	—
CAR2/MEY	0.0	0.7	<u>74.9</u>	—	0.1
CAR3/STR	<u>43.9</u>	32.0	14.9	—	—

Underlined figures indicate the highest value in each F_1 hybrid

¹⁾0: Main culm

I: Primary tillers

II: Secondary tillers

III: Subsequent tillers

U: Tillers of unknown orders

(i) Self-pollination (Table 9a)

Five hybrids, DIS/TYP2, DUR2/STR, DUR3/STR, ORI/STR, and ORI/MEY set no seeds by self-pollination. The data of self-pollination are not available in DIM/TYP1. In the other hybrids, fertility varied from 0.1% in DUR2/MEY to 23.9% in CAR2/STR.

Average of the fertility of whole hybrids in each heading period varied from 0.0% in whole April and the III of June to 8.5% in the I of June. The hybrids showed higher values in the later periods of their whole heading times, except for five hybrids, CAR1/TYP1, CAR1/STR, CAR2/STR, CAR2/MEY, and CAR3/STR. Three hybrids, CAR1/STR, CAR1/MEY, and CAR2/STR showed higher value more than 20% at least in one period. Furthermore, total fertility was more than 20.0% in two hybrids, CAR1/STR and CAR2/STR.

(ii) Open-pollination (Table 9b)

The fertility varied from 0.0% in one hybrid, DIM/TYP1 to 23.5% in CAR2/STR. The values were higher than those of self-pollination, except for in five hybrids, DIS/TYP3, DUR1/STR, DUR1/MEY, CAR1/TYP1, and CAR1/MEY.

Average of the fertility of whole hybrids in each heading period varied from 0.0% in whole April to 10.5% in the II of June. The hybrids showed higher values in the later periods of their whole heading times, except for six hybrids, DIS/TYP3, DUR1/STR, ORI/STR, ORI/MEY, CAR1/TYP1 and CAR3/STR.

(iii) Seed fertility in total (Table 10)

F₁ hybrids derived from three cross combinations, DIS/TYP3, DIS/STR, and DIM/STR showed relatively high pollen fertility (38.9%, 14.7% and 25.6%, respectively), but low seed fertility (8.0%, 1.4%, and 8.0%, respectively).

(b) Variation among florets

In case of the hybrids which produced seeds, F₁ plants set seeds both on the first and

Table 8. Pollen fertility (%) of each floret in a spike of CAR1/STR

Spikelet No. from the top	1st floret	2nd floret	3rd floret	4th floret
1	45.6	5.5	29.2	—
2	42.6	12.4	29.9	—
3	46.2	35.8	23.6	—
4	35.1	53.4	36.8	—
5	33.3	48.0	69.7	10.8
6	15.1	0.6	59.6	23.4
7	20.9	34.9	52.9	—
8	37.4	30.8	64.7	13.9
9	37.6	40.8	26.3	5.9
10	2.3	—	—	50.9
11	22.3	35.3	13.8	15.0
12	46.3	23.1	23.6	—
13	15.8	25.6	12.3	—
14	36.7	16.8	—	—

second florets. In some of them, seed set was observed on the third florets, and DUR2/STR set seeds even on the fifth florets. The first and second florets set seeds with higher frequencies than the other florets, except for one hybrid, ORI/STR.

(c) Seed fertility of the parental accessions

All the accessions showed higher values (>40.0%) than any hybrids. Although seed set was observed on the third florets in some accessions, it was mainly observed only on the first and second florets.

Discussion

(A) Factors affecting the crossability between parents

Six grades of crossability were arranged on the basis of difference of viability among the F₁ hybrids, as indicated in Table 5. Since viability was uniform within each F₁ hybrid, factors inducing its difference among hybrids are genetical. The crossability between tetraploid

Table 9. Self- and open-pollinated seed fertility (%) of the F₁ hybrids

(a) Self-pollination

Cross combination	Heading period										Overall average ^{1),2)}
	April			May			June			July	
	I	II	III	I	II	III	I	II	III	I	
DIS/TYP2	—	—	—	0.0	0.0	0.0	0.0	—	—	—	0.0
DIS/TYP3	—	—	—	8.2	—	<u>19.2</u>	—	—	—	—	10.0
DIS/STR	—	—	—	0.0	0.9	0.8	0.0	<u>4.3</u>	—	—	0.6
DIM/TYP1	—	—	—	—	—	—	—	—	—	—	—
DIM/STR	—	—	—	—	7.0	7.9	<u>8.1</u>	—	—	—	8.0
DUR1/STR	—	—	—	—	—	—	6.8	<u>16.7</u>	—	—	9.7
DUR1/MEY	—	—	—	—	—	—	—	<u>3.1</u>	0.0	—	2.2
DUR2/STR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	—	—	0.0
DUR2/MEY	—	—	0.0	0.0	0.0	0.0	<u>2.9</u>	0.0	—	—	0.1
DUR3/STR	—	—	—	—	—	0.0	0.0	—	—	—	0.0
OIR/STR	—	—	—	—	0.0	0.0	—	—	—	—	0.0
ORI/MEY	—	—	—	—	0.0	—	0.0	—	—	—	0.0
CAR1/TYP1	—	—	—	—	—	<u>14.9</u>	0.0	—	—	—	12.6
CAR1/STR	—	—	—	18.1	<u>30.2</u>	14.5	18.8	—	—	—	20.5
CAR1/MEY	—	—	—	16.2	14.3	4.5	<u>46.8</u>	—	—	—	17.4
CAR2/STR	—	—	—	16.4	<u>29.7</u>	—	12.3	—	—	—	23.9
CAR2/MEY	—	—	—	—	<u>5.5</u>	0.6	0.0	—	—	—	2.2
CAR3/STR	—	—	—	11.1	<u>14.7</u>	10.3	—	—	—	—	12.8
Average	0.0	0.0	0.0	7.8	<u>8.5</u>	5.6	7.4	4.8	0.0	—	7.1 ³⁾

Underlined figures indicate the highest value in each F₁ hybrid.

¹⁾Data whose heading period was not identified were also included in calculation

²⁾Percent of total number of seeds set grains per total number of florets

³⁾Average of the overall averages

(b) Open-pollination

Cross combination	Heading period										Overall average ^{1),2)}
	April			May			June			July	
	I	II	III	I	II	III	I	II	III	I	
DIS/TYP2	—	—	—	0.3	0.0	1.4	2.3	<u>4.3</u>	0.0	0.0	1.4
DIS/TYP3	—	—	—	<u>9.2</u>	—	4.5	0.0	—	—	—	6.6
DIS/STR	—	—	—	1.0	0.9	0.2	2.9	3.3	0.0	—	1.6
DIM/TYP1	—	—	—	—	—	0.0	—	—	—	—	0.0
DIM/STR	—	—	—	—	—	—	—	—	—	—	—
DUR1/STR	—	—	—	—	—	—	5.4	<u>6.4</u>	1.9	—	3.7
DUR1/MEY	—	—	—	—	—	—	—	0.0	0.6	<u>1.5</u>	0.6
DUR2/STR	—	0.0	0.0	0.0	0.2	0.1	<u>0.6</u>	0.2	0.0	0.0	0.2
DUR2/MEY	—	0.0	0.0	0.0	0.4	0.0	5.9	<u>8.8</u>	—	0.0	0.6
DUR3/STR	—	—	—	—	—	—	0.0	—	0.0	—	2.2
ORI/STR	—	—	—	—	<u>1.2</u>	0.2	0.0	0.0	0.0	—	0.2
ORI/MEY	—	—	—	—	—	<u>3.7</u>	1.0	0.0	—	—	0.6
CAR1/TYP1	—	—	—	—	<u>9.3</u>	2.6	2.3	—	—	—	1.9
CAR1/STR	—	—	—	19.7	20.6	24.4	19.8	<u>26.5</u>	25.0	—	22.2
CAR1/MEY	—	—	—	11.5	11.8	7.6	20.5	<u>33.0</u>	0.0	0.0	15.7
CAR2/STR	—	—	—	21.9	24.2	19.9	<u>27.6</u>	20.7	—	—	23.5
CAR2/MEY	—	—	—	—	9.2	8.1	8.7	<u>23.1</u>	—	—	10.4
CAR3/STR	—	—	—	—	<u>19.0</u>	18.6	—	—	—	—	21.7
Average	—	0.0	0.0	8.0	8.8	6.5	6.9	<u>10.5</u>	3.1	0.3	6.7 ³⁾

Underlined figures indicate the highest value in each F₁ hybrid.

¹⁾Data whose heading period was not identified were also included in calculation

²⁾Percent of total number of seeds set per total number of florets

³⁾Average of the overall averages

emmer wheats and *Ae. squarrosa* is summarized as follows;

- (1) TYP1, TYP2, and TYP3 (var. *typica*) possessed low affinity with tetraploid emmer wheats except for DIS. TYP1, however, possessed relatively higher affinity than the others. Whereas, STR (ssp. *strangulata*) and MEY (var. *meyeri*) possessed high affinity.
- (2) DIS (*T. dicoccoides*), DIM (*T. dicoccum*), and DUR2 (*T. durum*), and CAR1, CAR2, and CAR3 (*T. carthlicum*) possessed high affinity with STR (ssp. *strangulata*) or MEY (var. *meyeri*). Moreover, DIS possessed high affinity even with var. *typica*.

There were, however, a lot of factors involved in determination of crossability. As for the characteristics of dwarfness, following two kinds of factors are assumed;

- (1) those existing within STR (*Ae. squarrosa* ssp. *strangulata*) and MEY (var. *meyeri*), which are effective when crossed to DUR1, DUR3, or ORI.
- (2) those existing within TYP2 and TYP3 (var. *typica*), which are effective when crossed to CAR1, CAR2, or CAR3 (*T. carthlicum*).

Further investigations are necessary for more detailed analysis on these factors.

Table 10. Pollen and seed fertility (%) of the F₁ hybrids

(a) Pollen fertility

Female parents	Male parents				
	TYP1	TYP2	TYP3	STR	MEY
DIS	—	4.0(11.7)	38.9(52.6)	14.7(21.6)	—
DIM	—	—	—	25.6(37.2)	—
DUR1	—	—	—	—	1.5(1.5)
DUR2	—	—	—	0.6(8.1)	0.2(1.9)
DUR3	—	—	—	—	—
ORI	—	—	—	—	—
CAR1	—	—	—	36.0(60.8)	41.2(67.6)
CAR2	—	—	—	77.9(94.2)	16.1(74.9)
CAR3	—	—	—	33.4(84.1)	—

(b) Seed fertility in total¹⁾

Female parents	Male parents				
	TYP1	TYP2	TYP3	STR	MEY
DIS	—	1.1(4.3)	8.0(8.7)	1.4(3.5)	—
DIM	0.0(0.0)	—	—	8.0(8.1)	—
DUR1	—	—	—	4.6(7.6)	0.7(1.6)
DUR2	—	—	—	0.2(0.6)	0.4(6.6)
DUR3	—	—	—	1.5(0.0)	—
ORI	—	—	—	0.1(1.0)	0.6(3.7)
CAR1	4.7(10.9)	—	—	22.0(26.5)	15.9(33.0)
CAR2	—	—	—	23.5(26.1)	8.8(23.1)
CAR3	—	—	—	17.0(16.4)	—

Figures in parentheses indicate the highest value among the heading periods.

¹⁾Data whose heading period was not identified were also included in calculation.

(B) Factors affecting the ability of the formation of unreduced gametes in the F₁ hybrids

Relatively high pollen fertility but low seed fertility within a single hybrid as observed in three hybrids, DIS/TYP3, DIS/STR, and DIM/STR (Table 10) was also reported by KIHARA and LILIENFELD (1949) and KIHARA *et al.* (1965). In the present investigation, dehiscence of the anthers was observed except for in DIS/TYP3. Failure in fertilization or unsuccessful embryo development seemed to cause the low seed fertility.

Five crosses between CAR1, CAR2, or CAR3 and STR or MEY were the most successful, which showed high fertilities at least in one heading period. This result agrees well with previous reports. Taking fertility as well as viability of the hybrids into account, it is concluded that CAR1, CAR2, CAR3 (*T. carthlicum*), STR (ssp. *strangulata*) and MEY (var. *meyeri*) possess some genetic factors promoting the formation of unreduced gametes, as was reported by KIHARA, *et al.* (1965). These factors may not be a single gene, as reported in

case of *Secale cereale* (LELLY *et al.*, 1987). On the other hand, it is reported that there is (are) a gene or genes which prevent the production of diploid egg cells in durum wheat (JOPPA and WILLIAMS, 1987). Further experiments are necessary for detailed analysis of these factors.

The highest values of pollen and seed fertility in total in a hybrid were observed in almost the same heading periods, except for three hybrids, DIS, CAR1, or CAR3 / STR. In one hybrid DIS/STR, pollen fertility was observed only in the first one third of the periods where seed fertility was estimated. Another hybrid, CAR3/STR was the similar case. Further data are necessary to determine whether the two fertilities within these two hybrids had distinct peaks or not. Whereas in the hybrid CAR1/STR, there were two peaks both in pollen and in seed fertility in total, and the peaks of these fertilities coincided. Generally speaking, the highest values of pollen and seed fertility were expressed at almost the same time. Therefore, it is concluded that the formation of unreduced male and female gametes was coincidentally promoted.

The higher fertility in late-heading ears within the F_1 hybrids, as already reported (TABUSHI, 1956; KIHARA *et al.*, 1965), was observed in the present investigation. However, four hybrids, DIS/TYP3, ORI / STR or MEY, and CAR1/TYP1, the highest values were observed in the first half of the heading time. Except for one hybrid, DIS/TYP3, these hybrids showed characteristics of dwarfness. Late-heading ears of them were small and weak, and even moldy because of partial emergence of the spikes from flag leaf sheaths. So that, the low fertility observed in the late-heading ears of these hybrids seems to be due to the weakness of the plants. The hybrid, DIS/TYP3 showed the highest fertility in the first half of the heading time, but there was another peak in the second half. This hybrid also showed high value in late-heading ears. However, TABUSHI (1989) reported that there was no relationship between pollen fertility and heading date of the F_1 hybrids and that pollen fertility widely varied. In the present investigation, although such wide range of variation was observed (Table 8), the average of pollen fertility showed the tendency described above. Therefore, the phenomenon of high fertility in late-heading ears in the F_1 hybrids is concluded to be a general expression.

Seven hybrids, DIS/TYP2; DIS, DUR2, or CAR2 / STR; DUR2, CAR1, or CAR2 / MEY, showed higher pollen fertility in the secondary or subsequent tillers than in main culms or primary tillers. This is thought to be due to high temperature and/or some physiological factors. Irregular meiosis is induced by high temperature, for example as a result of decrease in the number of chiasmata in pollen mother cells in case of common wheat (BENNETT *et al.*, 1973). Late-heading ears in the present investigation underwent meiosis under high temperature. Therefore, it is difficult to determine which factor was the major one to promote high fertility in late-heading ears.

Various kinds of tetraploid emmer wheats as well as *Ae. squarrosa* must have been involved with the formation of bread wheat. It is sure that these species possessing the following abilities could produce more hexaploid progenies than the others;

- (1) ability to set enough F_1 seeds,
- (2) ability to produce viable F_1 plants,

(3) ability to produce abundant unreduced gametes on the F_1 hybrids.

These abilities were detected in the three accessions of *T. carthlicum*, one of *Ae. squarrosa* ssp. *strangulata* and var. *meyeri* used in the present investigation. And they were controlled by genetic factors. Thus, tetraploid emmer wheats and *Ae. squarrosa* which possessed such genetic factors must have played major roles on the formation of hexaploid bread wheat.

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二粒系コムギとタルホコムギのF₁における非還元配偶子形成を制御する因子に関する研究福多憲祐¹⁾・阪本寧男

(京都大学農学部附属植物生殖質研究施設, 京都府向日市物集女, 〒 617)

パンコムギ (ゲノム式: AABBDD) は, 二粒系コムギ (AABB) とタルホコムギ (DD) の雑種に生じた雌雄の非還元配偶子が受精した結果形成されたと考えられている. このことが木原 (1944) 及び MCFADDEN and SEARS (1944) によって明らかになって以来, 様々な系統を用いてパンコムギを合成する実験は行なわれたものの, 非還元配偶子形成に関する詳細な研究はなされてこなかった. そこで著者らは, (1) 非還元配偶子の形成過程を細胞学的に明らかにし, (2) 様々な条件下での形成頻度を求めることで, 非還元配偶子の形成機構の解明をはかった. そのうち, (1) の結果は育種学雑誌42: 255-266 (1992) で報告した. 本報では (2) の結果について報告する.

二粒系コムギ9系統とタルホコムギ5系統 (第1表) を交配し, F₁雑種を育成した. まず, これらの雑種の生育状況 (着粒率, 発芽率など) から, 親系統間の交雑親和性を推定した. 次に, 出穂したF₁について花粉稔性と種子稔性 (自家および放任受粉) を観察し, それをもって非還元配偶子形成頻度とした. 各々の稔性については, 親に用いた系統間, 異なる出穂期間, 及び個体内での変異を調査してその傾向を調査した.

上記の材料を用いて36組合せの交配を行なった結果, 33組合せでF₁種子が得られた (第2表). それらを育成したところ, 18組合せで出穂個体が得られたが, 他の組合せでは出穂前に全個体が枯死した (第5表). DIS (*Triticum dicoccoides*), CAR1, CAR 2, CAR 3 (いずれも *T. carthlicum*) を♀親に, STR (*Aegilops squarrosa* ssp. *strangulata*), MEY (*Ae. squarrosa* var. *meyeri*) を♂親に用いた場合, F₁の生育は良好であった (第5表).

花粉稔性は一般に以下の場合に高くなった. (1) ♀親にCAR1, CAR 2, CAR 3を, ♂親にSTR, MEYを用いた場合 (第6表, 第10表a). (2) 出穂期の後半で出穂した穂の場合 (第6表). (3) 高次分げつから出穂した穂の場合 (第7表). また, 1穂中の全小花について花粉稔性を調べた結果, かなりのばらつき (0.6-69.7%) がみられ, 必ずしも穂の中央部の第1小花の稔性が高いとは限らなかった (第8表). 種子稔性に関しても同様の傾向がみられた (第9表, 第10表b).

以上のことから, *T. carthlicum* と *Ae. squarrosa* ssp. *strangulata* または var. *meyeri* のF₁雑種における高い頻度の非還元配偶子形成は, 遺伝的に制御されているといえる. これらの間の交雑親和性の高さも考えに入れると, これらの系統の様な遺伝的要因を有する植物体が, 過去においてパンコムギの形成に重要な役割を演じたであろうと推測される. また, 出穂期の後半及び高次分げつで非還元配偶子形成頻度が高くなったが, これはこの雑種において一般的な現象であると考えられる.

¹⁾現住所: サッポロビール(株)植物工学研究所, 群馬県新田郡新田町木崎 37-1, 〒 370-03