M. Feldman

PHYLOGENETIC RELATIONSHIP AND SPECIES DIFFERENTIATION IN GENUS *TRITICUM* WITH SPECIAL REFERENCE TO THE GENOTYPES FOR DWARFNESS

By

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PHYLOGENETIC RELATIONSHIP AND SPECIES DIFFERENTIATION IN GENUS *TRITICUM* WITH SPECIAL REFERENCE TO THE GENOTYPES FOR DWARFNESS*

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(*With 17 Tables and 3 Figures*)

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* Contribution from the Laboratory of Genetics, Faculty of Agriculture, Kyoto University, No. 307.

Introduction

From morphological standpoint, Schulz (1913) classified wheat species into three groups, Einkorn, Emmer, and Dinkel groups. His classification has been supported by many investigations, especially by cytogenetical studies. Sakamura (1918) was the first author who found that 7, 14, and 21 are the haploid chromosome numbers of Einkorn, Emmer, and Dinkel wheats, respectively. His finding has also been confirmed by many studies later performed (Kihara 1919, 1924, Sax 1922, and others). Through the cytogenetical studies, the genome constitutions of these three groups of wheats were determined to be AA, AABB, and AABBDD, respectively (Kihara 1919, 1924). Afterwards the origin of the D genome was proved by Kihara (1944) and McFadden and Sears (1944). Namely, they proved that the D genome came from *Aegilops squarrosa*, an allied wild species. The ancestral genome of the B genome was recently estimated to have relations with the S-group genomes (Tanaka 1956, Sears 1956, Sarker and Stebbins 1956, and Riley et al. 1958).

However, definite informations are still lacking about the phylogenetical relationships in wheat species and the relatives.

The present study was started by the finding of the dwarf character by Kihara in 1947. The present author later found two complementary dwarf genes which make plants dwarf when they co-exist. It can be considered that these genes must have acted as an important isolation mechanism genetically. The significance of such complementary genes as an isolation mechanism has been already described by Stephens (1946, 1950) in *Gossipium*, as Dobzhansky (1951) recognized. Therefore, the present author investigated the distribution of these genes in natural species of wheats, intending to prove the phylogenetical relationships in wheats and the relatives.

Materials

The following species, varieties and artificial amphidiploids were used in the present investigation:

1. Emmer wheats ($2n=28$)
    - *T. dicoccoides* Körn. var. *spontaneo-nigrum* Flaksb.
    - *T. persicum* Vav. var. *stramineum* Zhuk.
    - *T. durum* Desf. var. *coerulescens* (Bayle) Körn.
    - *T. orientale* Perc.
2. Dinkel wheats ($2n=42$)
    - *T. vulgare* Vill. (*T. aestivum* L.)
        - var. *erythrospermum* Körn. No. 1
        - var. *alborubrum* Körn. No. 1
        - var. *albidum* Al. No. 1

  - var. *ferrugineum* Körn. No. 1
  - var. *lutescens* Al. No. 1 (Hohenheim) and No. 2
  - var. *erythroleucon* Körn. No. 1
  - var. *graecum* Körn. No. 1
  - var. (Thatcher)
  - var. (Timstein)
  - var. (Ceres)
  - var. (Nōrin 4)
  - var. (Chinese Spring) No. 1 and No. 2

T. spelta L.

  - var. *duhamelianum* Körn. No. 1
  - var. *vulpinum* Körn. No. 1
  - var. *arduini* Körn. No. 1

T. compactum Host

  - var. *icterinum* Al. No. 1
  - var. *humboldti* Körn. No 1
  - var. *fetisowii* Körn. No. 1
  - var. (WSC)
  - var. (KUSE No. 3063)
  - var. (KUSE No. 3065)

T. sphaerococcum Perc. *rubiginosum* Perc. No. 1

T. macha Dek. et Men. var. *sub-letschumicum* Dek. et Men. No. 1 and No. 2

T. macha Dek. et Men. var. *palaeo-imereticum* Dek. et Men. No. 1 and No. 2

3. Artificially synthesized $6x$ wheats ($2n=42$)

ABD No. 1 (*T. dicoccoides spontaneo-nigrum* + *Ae. squarrosa typica* No. 2), by Dr. Kihara et al.

ABD No. 2 (*T. durum coerulescens* + *Ae. squarrosa typica* No. 1 × No. 2), by Dr. Kihara et al.

ABD No. 3 (*T. turgidum nigrobarbatum* + *Ae. squarrosa typica* No. 2), by Dr. Kihara et al.

ABD No. 4 (*T. persicum stramineum* + *Ae. squarrosa typica* No. 2), by Dr. Kihara et al.

ABD No. 8 (*T. orientale* + *Ae. squarrosa typica* No. 2), by Dr. Kihara et al.

ABD No. 9 (*T. dicoccoides spontaneo-nigrum* + *Ae. squarrosa strangulata* No. 2124), by the author

ABD No.11 (*T. persicum stramineum* + *Ae. squarrosa typica* No. 2135), by the author

ABD No.17 (*T. persicum stramineum*

+ *Ae. squarrosa typica* No. 2107), by the author

ABD No.20 (*T. persicum stramineum*
+ *Ae. squarrosa typica* No. 2129), by the author

ABD No.22 (*T. persicum stramineum*
+ *Ae. squarrosa meyeri* No, 2124), by the author

ABD Sears (*T. dicoccum* (Vernal)
+ *Ae. squarrosa typica* (Sears)), by Dr. Sears

AAGGDD (*T. timopheevi*
+ *Ae. squarrosa typica* No. 2), by Dr. Watanabe

Gene analyses on dwarf wheats

1. Habit of plant growth in F_1

In the F_1 plants of *T. vulgare* var. *erythrospermum* or *T. spelta duhamelianum* × artificially synthesized hexaploid wheat ABD No. 1, and of its reciprocal cross, the growth rates and the general appearances of all the F_1 plants were almost normal as compared with the parents up to about 5 months after germination, namely in an early growth stage.

After 5 months, however, all the F_1 plants began to show dwarf character, and afterwards the leaf numbers of the dwarf plant increased, but the plant height did not extend. Accordingly, the bush-like habit of the F_1 plants continued up to the heading stage. At the heading stage, a few culms developed in some plants, and some seeds were set. But the F_1 plants often died before maturity. It is sure that these dwarf plants show very abnormal developments from morphological and physiological standpoints.

Besides, the culm length, ear size, ear length and others of the dwarf F_1 plants were very inferior as compared with those of their parents in almost all cases, as shown in Table 1.

Table 1. The plant heights and ear lengths of artificially synthesized hexaploid ABD No. 1, *T. spelta duhamelianum*, and the F_1's from the reciprocal crosses between them.

Parents or cross combinations	Plant heights (cm)	Ear lengths (cm)
ABD No. 1	85.0±5.00	12.25±0.43
T. spelta duhamelianum	127.5±3.94	12.17±0.76
ABD No. 1 × *T. spelta duhamelianum*	26.9±5.30*	4.33±2.57
Reciprocal	33.1±7.97*	4.60±1.96

* t=2.04, not significant at 5% level.

1a

1b

Fig. 1a. *T. spelta duhamelianum* (left), synthesized hexaploid ABD No. 1 (center), and the F_1 dwarf plant (right).

Fig. 1b. The F_1 dwarf plant in the field (the foremost row).

The dwarf F_1 plants and their parental plants are shown in Fig. 1a and 1b.

2. Segregations of the dwarf plants in F_2, F_3 and BF_1

The segregations of the dwarf plants in the F_2 progenies of the reciprocal crosses between ABD No. 1 and *T. spelta duhamelianum* or *T. vulgare erythrospermum* were as follows;

(1) 129 dwarfs: 84 normals from ABD No. 1 × *T. spelta duhamelianum*
(2) 105 dwarfs: 60 normals from *T. spelta duhamelianum* × ABD No. 1
(3) 122 dwarfs: 66 normals from ABD No. 1 × *T. vulgare erythrospermum*
(4) 152 dwarfs: 86 normals from *T. vulgare erythrospermum* × ABD No. 1

These segregation ratios are 1.54 : 1, 1.75 : 1, 1.86 : 1, and 1.77 : 1, respectively, giving an average of 1.72 : 1 (Table 2).

Table 2. Segregation of dwarf plants in the F_2's of *T. spelta duhamelianum* or *T. vulgare erythrospermum* × artificially synthesized hexaploid ABD No. 1.

Cross combinations	No. of plants observed in F_2		Dwarfs : Normals
	Dwarfs	Normals	
ABD No. 1 × *T. spelta duhamelianum*	129	84	1.54 : 1
Reciprocal	105	60	1.75 : 1
ABD No. 1 × *T. vulgare erythrospermum*	122	66	1.86 : 1
Reciprocal	152	86	1.77 : 1

In the F_3, on the other hand, the following four kinds of segregations were observed;

(1) All the normal F_2 plants gave only normals.
(2) All the dwarf F_2 plants gave both dwarfs and normals, but three different segregations were observed, i. e.,
  i) about the same segregation with the 1.72 : 1 in ratio F_2.
  ii) more dwarfs than in F_2.
  iii) less dwarfs than in F_2.

Table 3. Segregations of dwarf plants in the reciprocal crosses between (*T. spelta duhamelianum* × ABD No. 1) F_1 and *T. spelta duhamelianum*.

Cross combinations	Normals	Dwarfs	χ^2 test for 1 : 1 ratio
(*T. spelta* × ABD No. 1) F_1 × *T. spelta*	40 (1 :	42 1.05)	$\chi^2=0.046$ $P>0.05$
T. spelta × (*T. spelta* × ABD No. 1) F_1	7 (1 :	19 2.71)	$\chi^2=5.538$ $P<0.02$ $P>0.01$

From this result, it is possible to consider that the dwarf character is controlled by two dominant genes.

In order to obtain further informations on the genetic behavior of the dwarfness, reciprocal backcrosses were carried out between the above F_1 plants and *T. spelta duhamelianum*. The segregations obtained in the BF_1 are presented in Table 3. It is clear that F_1 × *T. spelta* gave dwarfs and normals in 1 : 1 ratio, but that *T. spelta* × F_1 gave more dwarfs in a ratio of about 2.7 : 1. It is supposed that the latter ratio may have relation with a competitive fertilization.

3. Determined dwarf genes and the genetic behavior

From the results obtained in the F_1, F_2, F_3, and BF_1, it can be concluded that two complementary dominant genes control the dwarf character. The genes were designated Dw_1 and Dw_2. Namely, the genotype given to ABD No. 1 is $Dw_1Dw_1dw_2dw_2$, and those given to *T. spelta duhamelianum* and *T. vulgare erythrospermum* are both $dw_1dw_1Dw_2Dw_2$. It was considered that the co-existence of Dw_1 and Dw_2 makes the plants dwarf, namely, that the plants having both dominant genes become dwarf. Therefore, the F_1 plants between above ABD No. 1 and above *T. spelta* or *T. vulgare* must have the genotype $Dw_1dw_1Dw_2dw_2$. From the F_1, the following genotypes are expected in the F_2, in the ratio as shown;

Dwarfs : 1 $Dw_1Dw_1Dw_2Dw_2$
2 $Dw_1Dw_1Dw_2dw_2$
2 $Dw_1dw_1Dw_2Dw_2$
4 $Dw_1dw_1Dw_2dw_2$

Normals : 1 $Dw_1Dw_1dw_2dw_2$
2 $Dw_1dw_1dw_2dw_2$
1 $dw_1dw_1Dw_2Dw_2$
2 $dw_1dw_1Dw_2dw_2$
1 $dw_1dw_1dw_2dw_2$

From this expectation, the segregation in the F_2 must be 9 dwarfs : 7 normals (= 1.29 : 1). The present observed data, 1.72 dwarfs : 1 normals are, considerably apart from the expectation.

On the other hand, the following genotypes are expected in the BF_1 from F_1 × *T. spelta* or the reciprocal cross;

Dwarfs : 1 $Dw_1dw_1Dw_2Dw_2$
1 $Dw_1dw_1Dw_2dw_2$

Normals : 1 $dw_1dw_1Dw_2Dw_2$
1 $dw_1dw_1Dw_2dw_2$

The experimental result from F_1 × *T. spelta* fits well to the expectation, but that from *T. spelta* × F_1 does not fit. Although the observed number in the latter cross was not enough because the F_1 dwarf plants were too feeble to produce good pollen, the ratio of dwarfs : normals equals 2.71 : 1 as seen in Table 3.

Supposing that the ratio, 2.71 : 1 was due to the competition among four kinds of pollen having Dw_1Dw_2, Dw_1dw_2, dw_1Dw_2, and dw_1dw_2 genotypes from the F_1 plants, it would be able to give an explanation to the present data in the F_2, F_3 as well as the BF_1. That is to say, it can be supposed that the Dw_1-carrying pollen (Dw_1Dw_2 and Dw_1dw_2) could participate in fertilization about 2.7 times more frequently than the dw_1-carrying pollen (dw_1Dw_2 and dw_1dw_2). In this case, it is supposed that there is no competition among female gamates. Furthermore, from the fact that there was no F_2 dwarf plant which bred true for the dwarfness, it is conclusive that the $Dw_1Dw_1Dw_2Dw_2$ genotype makes the embryo completely lethal, and no such plant can emerge.

From the above supposition and conclusion, the segregation ratio in the F_2 must be as follows;

Dwarfs : 5.4 $Dw_1Dw_1Dw_2dw_2$
3.7 $Dw_1dw_1Dw_2Dw_2$
7.4 $Dw_1dw_1Dw_2dw_2$

Normals : 2.7 $Dw_1Dw_1dw_2dw_2$
3.7 $Dw_1dw_1dw_2dw_2$
1 $dw_1dw_1Dw_2Dw_2$
2 $dw_1dw_1Dw_2dw_2$
1 $dw_1dw_1dw_2dw_2$

Namely, a ratio of 16.5 dwarfs : 10.4 normals (≒1.6 : 1) is calculated. The observed segregation ratios in the F_2 described above, i.e. 1.54∼1.86 : 1, are considerably close to this expectation from the above supposition. A statistical test was carried out on the fitness of the observed ratios to the expected one, and very satisfying results were obtained (Table 4).

Table 4. Segregation ratios of dwarfness in the F_2 generation in the reciprocal crosses between ABD No. 1 and *T. spelta* or *T. vulgare*.

Cross combination	No. of plants	Expected no. of plants from 1.6 : 1	χ^2, P
ABD No. 1 × *T. spelta duham.*	dwarf 129 normal 84	131.1 81.9	$\chi^2=0.0875$ $P>0.05$
reciprocal	dwarf 105 normal 60	101.5 63.5	$\chi^2=0.3136$ $P>0.05$
ABD No. 1 × *T. vulgare eryth.*	dwarf 122 normal 66	115.7 72.3	$\chi^2=0.8920$ $P>0.05$
reciprocal	dwarf 152 normal 86	146.5 91.5	$\chi^2=0.5371$ $P>0.05$

Therfore, the following conclusions are given; (1) The dwarfness described in the present paper is controlled by two complementary genes, Dw_1 and Dw_2. (2) ABD No. 1 has the $Dw_1Dw_1dw_2dw_2$ genotype, while *T. spelta duhamelianum* and *T. vulgare erythrospermum* have the $dw_1dw_1Dw_2Dw_2$ genotype. Thus, the F_1 plants between the former and the latters are $Dw_1dw_1Dw_2dw_2$, and they show the dwarf phenotype. (3) The $Dw_1Dw_1Dw_2Dw_2$ zygotes are completely lethal, thus, no dwarf plant which breeds

Table 5. Segregation ratios in the selfed progenies of the heterozygous plants for complementary dwarf genes.

Parental genotypes		Segregations in selfed progenies		Segregation ratios (Normals : Dwarfs)
		Normals	Dwarfs	
Normals	$Dw_1dw_1dw_2dw_2$	2.7 $Dw_1Dw_1dw_2dw_2$ 3.7 $Dw_1dw_1dw_2dw_2$ 1 $dw_1dw_1dw_2dw_2$		1 : 0
	$dw_1dw_1Dw_2dw_2$	1 $dw_1dw_1Dw_2Dw_2$ 2 $dw_1dw_1Dw_2dw_2$ 1 $dw_1dw_1dw_2dw_2$		1 : 0
Dwarfs	$Dw_1Dw_1Dw_2dw_2$	1 $Dw_1Dw_1dw_2dw_2$	2 $Dw_1Dw_1Dw_2dw_2$	1 : 2
	$Dw_1dw_1Dw_2Dw_2$	1 $dw_1dw_1Dw_2Dw_2$	3.7 $Dw_1dw_1Dw_2Dw_2$	1 : 3.7
	$Dw_1dw_1Dw_2dw_2$	2.7 $Dw_1Dw_1dw_2dw_2$ 3.7 $Dw_1dw_1dw_2dw_2$ 2 $dw_1dw_1Dw_2dw_2$ 1 $dw_1dw_1dw_2dw_2$ 1 $dw_1dw_1Dw_2Dw_2$	5.4 $Dw_1Dw_1Dw_2dw_2$ 3.7 $Dw_1dw_1Dw_2Dw_2$ 7.4 $Dw_1dw_1Dw_2dw_2$	1 : 1.6

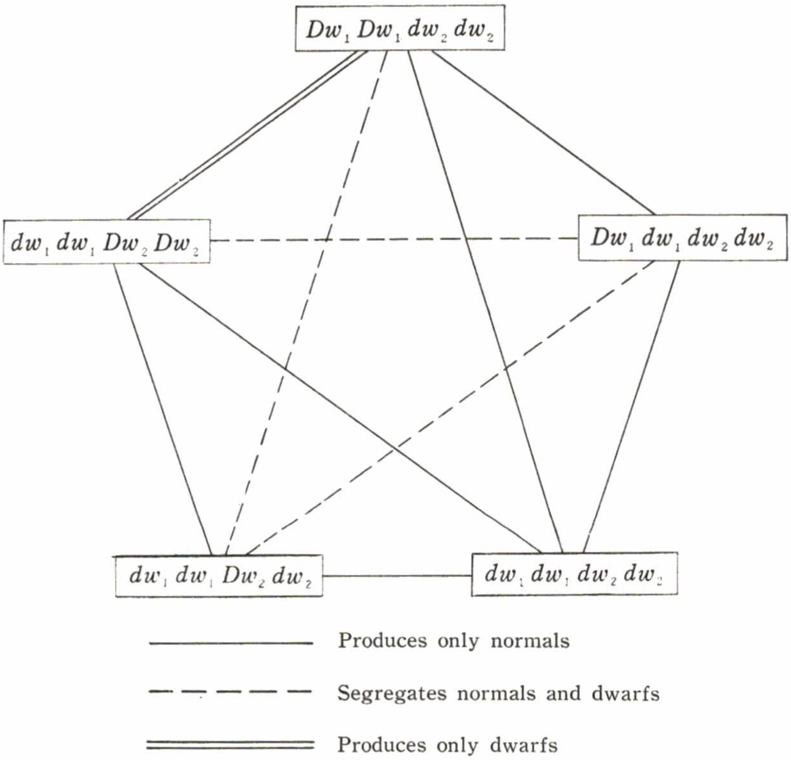

Fig. 2. Appearance of dwarf plants in the F_1 hybrids between normal-type plants.

true appears. (4) A competitive fertilization occurs between the Dw_1-carrying pollen and the dw_1-carrying pollen, giving a ratio, of 2.7 : 1. Therefore, the segregations in the BF_1 from *T. spelta duhamelianum* × F_1 and in the F_2 are distorted as shown in Tables 2 and 3.

From these results, segregation ratios from various heterozygotes for the dwarf genes can be expected as shown in Table 5. Almost all of the data obtained in the present study showed good fitness with the expected ratios.

There are five possible genotypes which lead to normal phenotype, i. e., $Dw_1Dw_1dw_2dw_2$, $Dw_1dw_1dw_2dw_2$, $dw_1dw_1Dw_2Dw_2$, $dw_1dw_1Dw_2dw_2$, and $dw_1dw_1dw_2dw_2$. Of course, there must be only three homozygous genotypes in natural species or varieties, i. e., the first, third and fifth of above genotypes. The segregations of dwarfs and normals in ten possible cross combinations among these five genotypes were shown in Fig. 2.

4. Analysing method of unknown genotypes for the dwarfness

The above experimental results made it possible to analyse the genotypes for the dwarfness of various strains of Dinkel wheats. Namely, unknown genotypes will be clarified by the investigation on the habits of plant growth of the F_1 plants between the plants with unknown genotypes and two tester plants, ABD No. 1 ($Dw_1Dw_1dw_2dw_2$) and *T. spelta duhamelianum* ($dw_1dw_1Dw_2Dw_2$). The analysing method is as follows (see also Table 6) ;

(1) If the F_1 plants between a strain and ABD No. 1 are normal, but the F_1's between the strain and *T. spelta duhamelianum* are dwarf, the strain must have the $Dw_1Dw_1dw_2dw_2$ genotype.

(2) If the reverse relationship is observed in case of another strain, the strain must have the $dw_1dw_1Dw_2Dw_2$ genotype.

(3) If the F_1's from the crosses of a strain to both tester plants are both normal, the strain must have the $dw_1dw_1dw_2dw_2$ genotype.

This method was used in the following experiments.

Table 6. Analysing method of unknown genotypes for the dwarfness.

♀		Plants with unknown genotypes		Genotypes determined
♂		*T. spelta duhamelianum* ($dw_1dw_1Dw_2Dw_2$)	ABD No. 1 ($Dw_1Dw_1dw_2dw_2$)	
Phenotypes of F_1	I	dwarf	normal	$Dw_1Dw_1dw_2dw_2$
	II	normal	dwarf	$dw_1dw_1Dw_2Dw_2$
	III	normal	normal	$dw_1dw_1dw_2dw_2$

Distribution of the genotypes for the dwarfness in wheats

1. Distribution in Dinkel wheats

Twenty six strains belonging to five species of Dinkel wheat were crossed to two testers, *T*, *spelta duhamelianum* and artificially synthesized hexaploid wheat, ABD No. 1. Phenotypes of the F_1 plants from these crosses are summarized in Table 7. The genotype for the dwarfness of each variety was determined from the present experiment and is also given in the same table.

Table 7. Phenotypes for the dwarfness of the F_1's between two testers and various varieties of Dinkel wheat.

Tested species and varieties	Testers (genotypes)		Genotypes of tested species
	T. spelta ($dw_1dw_1Dw_2Dw_2$)	ABD No. 1 ($Dw_1Dw_1dw_2dw_2$)	
T. vulgare			
var. *alborubrum* No. 1	+	—	$dw_1dw_1Dw_2Dw_2$
var. *albidum* No. 1	+	—	〃
var. *ferugineum* No. 1	+	—	〃
var. *lutescens* No. 2	+	—	〃
Thatcher	+	—	〃
Timstein	+	—	〃
Chinese Spring No. 1 and No. 2	+	—	〃
var. *erythroleucon* No. 1	+	+	$dw_1dw_1dw_2dw_2$
var. *graecum*	+	+	〃
var. *lutescens* No. 1	+	+	〃
Ceres	—	+	$Dw_1Dw_1dw_2dw_2$
Nōrin 4	—	+	〃
T. spelta			
var. *vulpinum* No. 1	+	—	$dw_1dw_1Dw_2Dw_2$
var. *arduini* No. 1	+	—	〃
T. compactum			
var. *humboldti* No. 1	+	—	$dw_1dw_1Dw_2Dw_2$
WSC	+	—	〃
KUSE No. 3063	+	—	〃
〃 No. 3065	+	—	〃
var. *icterinum* No. 1	+	+	$dw_1dw_1dw_2dw_2$
var. *fetisowii* No. 1	+	+	〃
T. sphaerococcum			
var. *rubiginosum* No. 1	+	—	$dw_1dw_1Dw_2Dw_2$
T. macha			
var. *sub-litschumicum* No. 1	+	—	$dw_1dw_1Dw_2Dw_2$
var. 〃 No. 2	+	+	$dw_1dw_1dw_2dw_2$
var. *paleo-imereticum* No. 1 and No. 2	+	+	〃

+ : normal — : dwarf

Table 8. Number of strains of Dinkel wheats having each of three genotypes for the dwarfness.

Species	Genotypes			Total
	$Dw_1Dw_1dw_2dw_2$	$dw_1dw_1dw_2dw_2$	$dw_1dw_1Dw_2Dw_2$	
T. vulgare	2	3	8	13
T. compactum	0	2	4	6
T. spelta	0	0	2	2
T. sphaerococcum	0	0	1	1
T. macha	0	3	1	4
Total	2	8	16	26

As Table 8 shows, the majority of Dinkel wheats used have the genotype $dw_1dw_1Dw_2Dw_2$, but some varieties of *T. vulgare* and *T. compactum* have either $dw_1dw_1dw_2dw_2$ or $Dw_1Dw_1dw_2dw_2$. There was no variety which has the $Dw_1Dw_1Dw_2Dw_2$ genotype. In *T. macha*, the genotype $dw_1dw_1dw_2dw_2$ was found in three out of four strains used.

2. Distribution in artificially synthesized hexaploid wheats

Twelve strains of artificially synthesized hexaploids were crossed to the two testers, as in the previous experiment. Appearances of dwarfness in the F_1 plants are summarized in Table 9. The genotype for the dwarfness of each strain was determined from this experiment and is also given in the same table.

Furthermore, in order to test if the determined genotypes are correct, interstrain hybrids of 15 different combinations were made. The observed results in this ex-

Table 9. Phenotypes for the dwarfness of the F_1's between two testers and artificially synthesized hexaploids.

Strains No.	Testers (genotypes)		Genotypes of tested strains
	T. spelta ($dw_1dw_1Dw_2Dw_2$)	ABD No. 1 ($Dw_1Dw_1dw_2dw_2$)	
ABD No. 1	—	+	$Dw_1Dw_1dw_2dw_2$
〃 2	+	—	$dw_1dw_1Dw_2Dw_2$
〃 3	+	+	$dw_1dw_1dw_2dw_2$
〃 4	+	+	〃
〃 8	—	+	$Dw_1Dw_1dw_2dw_2$
〃 9	—	+	〃
〃 11	+	—	$dw_1dw_1Dw_2Dw_2$
〃 17	+	—	〃
〃 20	+	—	〃
〃 22	+	—	〃
〃 Sears	+	+	$dw_1dw_1dw_2dw_2$
AAGGDD	—	+	$Dw_1Dw_1dw_2dw_2$

+ : normal — : dwarf

periment well fit the results from the former experiment for the genotypes (Tables 10 and 11).

From the determined genotypes, the artificially synthesized hexaploids are divided into three groups as follows:

Table 10. Observations on the dwarfness in the F_1's of interstrain cross-combinations in artificially synthesized hexaploids.

Cross combinations	Number of plants observed in F_1's	
	Normal plants	Dwarf plants
ABD No. 1 × ABD No. 2	0	11
〃 × 〃 3	18	0
〃 × 〃 4	12	0
〃 × 〃 8	7	0
〃 × 〃 Sears	25	0
ABD No. 2 × ABD No. 3	29	0
〃 × 〃 4	13	0
〃 × 〃 8	0	15
〃 × 〃 Sears	27	0
ABD No. 3 × ABD No. 4	7	0
〃 × 〃 8	3	0
〃 × 〃 Sears	28	0
ABD No. 4 × ABD No. 8	4	0
〃 × 〃 Sears	30	0
ABD No. 8 × ABD Sears	12	0

Table 11. Phenotypes for the dwarfness of interstrain hybrids in artificially synthesized hexaploids.

	$Dw_1Dw_1dw_2dw_2$	$dw_1dw_1Dw_2Dw_2$	$dw_1dw_1dw_2dw_2$	$dw_1dw_1dw_2dw_2$	$Dw_1Dw_1dw_2dw_2$	$dw_1dw_1dw_2dw_2$
	ABD No. 1	ABd No. 2	ABD No. 3	ABD No. 4	ABD No. 8	ABD Sers
$Dw_1Dw_1dw_2dw_2$ ABD No. 1	+	−	+	+	+	+
$dw_1dw_1Dw_2Dw_2$ 〃 2		+	+	+	−	+
$dw_1dw_1dw_2dw_2$ 〃 3			+	+	+	+
$dw_1dw_1dw_2dw_2$ 〃 4				+	+	+
$Dw_1Dw_1dw_2dw_2$ 〃 8					+	+
$dw_1dw_1dw_2dw_2$ 〃 Sears						+

+ : normal − : dwarf

Group 1 ($Dw_1Dw_1dw_2dw_2$)	ABD No. 1
	ABD No. 8
	ABD No. 9
	AAGGDD
Group 2 ($dw_1dw_1Dw_2Dw_2$)	ABD No. 2
	ABD No. 11
	ABD No. 17
	ABD No. 20
	ABD No. 22
Group 3 ($dw_1dw_1dw_2dw_2$)	ABD No. 3
	ABD No. 4
	ABD Sears

Origin of dwarf genes

The origin of the complementary genes, Dw_1 and Dw_2, was considered from the results obtained in the following experiments.

1. Interspecific hybrids between Emmer wheats

Interspecific crosses were performed between the Emmer wheats, the genotypes

Table 12. Habits of plant growth in F_1 interspecific hybrids between Emmer wheats.

Cross combinations	Habits of plant growth in F_1's
T. dicoccoides spontaneo-nigrum × *T. persicum stramineum*	Normal
Reciprocal	〃 (slightly low)
T. dicoccoides spontaneo-nigrum × *T. orientale*	〃
Reciprocal	〃 (slightly low)
T. dicoccoides spontaneo-nigrum × *T. durum coerulescens*	〃 (slightly low)
Reciprocal	〃
T. persicum stramineum × *T. orientale*	〃 (slightly low)
Reciprocal	〃

for the dwarfness of which had already been clarified in the artificially synthesized hexaploid wheats from them and *Ae. squarrosa*. These Emmer wheats were *T. dicoccoides spontaneo-nigrum*, *T. durum coerulescens*, *T. persicum stramineum* and *T. orientale*. The interspecific hybrids between them were investigated whether they are dwarf or not. It was made clear that no dwarf plant was found in every combination of the interspecific crosses (Table 12).

The present result well accords with the fact that dwarf F_1 plant has never been observed in various interspecific crosses between Emmer wheats performed by many workers. Therefore, it is concluded that both Dw_1 and Dw_2 genes do not co-exist in wheats belonging to Emmer group.

2. Intraspecific (intervariety and interstrain) hybrids of *Ae. squarrosa*

Intervariety and interstrain hybrids of 28 different combinations were made using 25 strains belonging to 4 varieties of *Ae. squarrosa*. These strains were selected from geographical and taxonomical standpoints out of total 176 strains of *Ae. squarrosa* which had been collected from various places of the distribution area of this species (Kihara and Tanaka 1958). All the hybrids were of normal type without any exception. It is conclusive, therefore, that both dominant genes, Dw_1 and Dw_2, do not co-existing in *Ae. squarrosa*.

On the other hand, both dominant genes are found among Dinkel wheats and also among artificially synthesized hexaploid wheats. Therefore, from above conclusions, one of the dominant genes must have been derived from Emmer wheat and another from *Ae. squarrosa*. Namely, it can be assumed that the Dw_1-dw_1 genes are present in either A or B genome and the Dw_2-dw_2 genes in D genome.

3. Origin of dwarf genes estimated from the genotypes for the dwarfness of synthesized hexaploid wheats

Standing on the above assumption, the origin of the dwarf genes can be estimated from the genotypes for the dwarfness of synthesized hexaploid wheats. The relationships of the genotypes of these synthesized wheats to the parental Emmer wheats and *Ae. squarrosa* are presented in Table 13. There are three genotypes, $Dw_1Dw_1dw_2dw_2$, $dw_1dw_1Dw_2Dw_2$, and $dw_1dw_1dw_2dw_2$, in these synthesized wheats. From this table the genotypes of the parental Emmer wheats and *Ae. squarrosa* can be estimated.

Concerning the Dw_1 and dw_1 genes, the parental Emmer wheats can be classified into two groups, Dw_1 group (the first group in Table 13) and dw_1 group (the second and third groups in Table 13). *T. dicoccoides spontaneo-nigrum* and *T. orientale* belong to the Dw_1 group, and *T. durum coerulescens*, *T. persicum stramnieum*, *T. turgidum nigrobarbatum*, and *T. dicoccum* (Vernal) belong to the dw_1 group. There is no Emmer wheat species which belongs to both groups. The estimated

Table 13. Genotypes for the dwarfness and the parents of artificially synthesized hexaploids.

Groups	Genotypes	Artificially synthesized hexaploids	Emmer wheats (Dw_1-dw_1)	*Ae. squarrosa* (Dw_2-dw_2)
I	$Dw_1Dw_1dw_2dw_2$	ABD No. 1	*T. dicoccoides spontaneo-nigrum*	var. *typica* No. 2
		〃 8	*T. orientale*	〃
		〃 9	*T. dicoccoides spontaneo-nigrum*	var. *strangulata* No. 2124
		AAGGDD	*T. timopheevi*	var. *typica* No. 2
II	$dw_1dw_1Dw_2Dw_2$	ABD No. 2	*T. durum coerulescens*	var. *typica* No. 1 × No. 2
		〃 11	*T. persicum stramineum*	var. *strangulata* No. 2135
		〃 17	〃	var. *typica* No. 2107
		〃 20	〃	〃 No. 2129
		〃 22	〃	var. *meyeri* No. 2144
III	$dw_1dw_1dw_2dw_2$	ABD No. 3	*T. turgidum nigrobarbatum*	var. *typica* No. 2
		〃 4	*T. persicum stramineum*	〃
		〃 Sears	*T. dicoccum* (Vernal)	〃 Sears

genotypes of these Emmer wheats are shown in Table 14, together with the distributions. As seen in this table, a wild species (*T. dicoccoides*) has the dominant gene and many cultivated species have the recessive gene. As an exceptional case, *T. orientale*, which has been regarded as a cultivated species, has the Dw_1 gene. However, the originated district and the taxonomical position of this species have not yet been clarified. Although Vavilov et al. (1931) regarded it as one variety of *T. durum*, *T. orientale* rather resembles *T. dicoccoides* as to the kernel form and some other morphological characters. That the Dw_1 gene is present in *T. orientale* as well as in *T. dicoccoides* is a remarkable fact.

Concerning Dw_2 and dw_2, on the other hand, seven strains of *Ae. squarrosa* used for synthesizing hexaploid wheats can be classified into two groups, Dw_2 group (the second group in Table 13) and dw_2 group (the first and third groups in Table

Table 14. Distribution of dwarf genes, Dw_1 and dw_1, in Emmer wheats.

Genotypes	Species and varieties	Centers of geographical distributions
Dw_1Dw_1	*T. dicoccoides spontaneo-nigrum*	Armenia and Palestine
	T. timopheevi	western Georgia
	T. orientale	Mediterranean area
dw_1dw_1	*T. durum coerulescens*	Mediterranean area and Abyssinia
	T. persicum stramineum	Armenia
	T. persicum fuliginosum	〃
	T. turgidum nigrobarbatum	Mediterranean area
	T. dicoccum (Vernal)	Armenia and Abyssinia

13). In case of the synthesized ABD No. 2, an F_1 plant from No. 1 strain × No. 2 strain of *A. squarrosa typica* had been used as the father plant, but it is presumed that the Dw_2 gene which had been present in the No. 1 strain was transmitted from the F_1 plant in this case, considering the cases in which the No. 2 strain had been used. The estimated genotypes and the distributions of these strains of *Ae. squarrosa* are presented in Table 15. So far as the present result is concerned, it is obvious that both of the Dw_2Dw_2 and dw_2dw_2 genotypes are present even in the same variety of this species, but not in the same strain. Besides, it may be possibe to say that the Dw_2 gene is more widely distributed than the recessive allele, dw_2. As Table 15 shows, two strains of *Ae. squarrosa strangulata* used, No. 2124 and No. 2135, are those collected from adjacent places, but they have different genotypes. Thus, there is a possibility of co-existence of the dominant and recessive genes in a district.

Table 15. Distribution of dwarf genes, Dw_2 and dw_2, in *Aegilops squarrosa*.

Genotypes	Varieties		Haibtats collected in
Dw_2Dw_2	var. *typica*	No. 1	Derbent, Caucasus
	〃	No. 2107	Karaj, Iran
	〃	No. 2129	Khoshyailagh, Iran
	var. *strangulata*	No. 2135	Beshahr, Iran
	var. *meyeri*	No. 2144	Ramsar, Iran
dw_2dw_2	var. *typica*	No. 2	Palestine ?[1]
	var. *strangulata*	No. 2124	Gorgan-Khoshyailagh, Iran

[1] According to Eig (1929), *Ae. squarrosa* does not exist in Palestine, whereas after Kappert (1934) this species is found there. I am not sure, whether or not the strain No. 2 was originally collected in Palestine.

Through these investigations, it can be concluded that the Dw_1-dw_1 genes in Emmer wheats and the Dw_2-dw_2 genes in *Ae. squarrosa* were combined at the time when Dinkel wheats were formed, and that they began to act as complementary genes at that time.

In the natural world, the following phenomena must have occurred: (1) Three types of Dinkel wheats having $Dw_1Dw_1dw_2dw_2$, $dw_1dw_1Dw_2Dw_2$, and $dw_2dw_2dw_2dw_2$ genotypes for dwarfness must have originated from Emmer wheats and *Ae. squarrosa*, and that having $Dw_1Dw_1Dw_2Dw_2$, if formed, must have died. (2) If the Dinkel wheats of the $Dw_1Dw_1dw_2dw_2$ and $dw_1dw_1Dw_2Dw_2$ types had been co-existing, the hybrids between them, if produced, must have died. Namely, these two types must have been isolated genetically one another. (3) On the other hand, normal hybrids must have been produced between the $dw_1dw_1dw_2dw_2$ type and other two types. Therefore, the $dw_1dw_1dw_2dw_2$ type wheats must have acted as a bridge between the $Dw_1Dw_1dw_2dw_2$

and $dw_1dw_1Dw_2Dw_2$ types, to exchange their genetic materials.

The above relationships suggest that the dwarf genes are important tracers to investigate the origin and the phylogenetic relationship of hexaploid wheats.

4. Dwarf gene in *timopheevi* wheat

Two tester plants, the synthesized ABD No. 1 hexaploid wheat ($Dw_1Dw_1dw_2dw_2$) and *T. spelta duhamelianum* ($dw_1dw_1Dw_2Dw_2$), were crossed to a synthesized hexaploid wheat, AAGGDD plant obtained from *T. timopheevi* No. 1 × *Ae. squarrosa typica* No. 2. The F_1 plants from AAGGDD × ABD No. 1 were normal but those from AAGGDD × *T. spelta* were dwarf. As *Ae. squarrosa typica* No. 2 has the dw_2 gene, this result clearly proves that the Dw_1 gene exists in the genomes of *T. timopheevi*. The fact that *T. timopheevi* used has the Dw_1 gene is very interesting considering that *T. dicoccoides* also has the dominant gene.

5. Function of dwarf genes in pentaploid hybrids

It is possible to obtain $Dw_1dw_1Dw_2$ pentaploid hybrids from some adequate cross combinations, for example, such as *T. dicoccoides spontaneonigrum* (Dw_1Dw_1) × *T. spelta duhamelianum* ($dw_1dw_1Dw_2Dw_2$). The $Dw_1dw_1Dw_2$ plants were expected to be dwarf, because they had both dominant genes, Dw_1 and Dw_2. Against the expectation, however, the F_1 pentaploid hybrids between the above *T. dicoccoides* or *T. orientale* (Dw_1Dw_1) and the above *T. spelta* were not dwarf (Table 16).

Table 16. Phenotypes for the dwarfness of pentaploid hybrids, Dw_1Dw_1 × $dw_1dw_1Dw_2Dw_2$.

Cross combinations	Phenotypes in the F_1's
T. dicoccoides spontaneo-nigrum (Dw_1Dw_1) × *T. spelta duhamelianum* ($dw_1dw_1Dw_2Dw_2$)	normal
T. orientale (Dw_1Dw_1) × *T. spelta duhamelianum* ($dw_1dw_1Dw_2Dw_2$)	normal

The following two interpretations will be made as to this unexpected result: (1) The complementary genes, Dw_1 and Dw_2, can not express their effect in hemizygous condition, even if both dominant genes are co-existing. There have been reported some instances showing the differences in genetic effect between hemizygous and homo- or heterozygous conditions (Stern 1943 and Sears 1954). (2) The Dw_1 and Dw_2 genes were not present in Emmer wheats and *Ae. squarrosa*. But such complementary genes were newly produced when Dinkel wheats were formed. Therefore, no dwarf F_1 plant is produced from Emmer × Dinkel.

Sachs (1953) proposed the second interpretation. However, it seems improbable that mutations occurred in very high frequency at the time of formation of polyploid plants. Furthermore, it is very difficult to explain by the second interpretation the fact that hexaploid wheats produced from the same combination of tetraploid wheat and *Ae. squarrosa* always have the same genotype for the dwarfness.

Therefore, the first interpretation seems more appropriate than the second one. But it remains uncertain why the Dw_2 gene can not express the genetic function in hemizygous condition.

Discussion

The significance of complementary lethal genes existing in a population of organisms is, as already mentioned, that an isolation mechanism is established by the genes in the population. This has been already described by Stephens (1946, 1950). He reported that a lethal phenomenon was observed in the hybrids between *Gossipium barbadense* and some strains of *G. hirsutum*, and that the phenomenon was controlled by two complementary genes. He further made it clear that the complementary genes are distributed only in the district where both species are found. As Dobzhansky (1951) stated, this is a good example showing that complementary genes establish an isolation mechanism.

The complementary dwarf genes, Dw_1 and Dw_2, described in the present paper, also make the plants lethal or extremely dwarf and induce serious physiological disturbances, if both the genes co-exist. Thus, the plants having both the genes hardly give the offsprings. Especially, the plants which are homozygous for both the dominant genes, i.e., $Dw_1Dw_1Dw_2Dw_2$, are completely lethal.

This complementary gene system must have acted as an effective isolation mechanism since it had been completed. It is certain that the isolation mechanism would have been preserved until now. Therefore, these genes can be used to trace the phylogenetic relationship in genus *Triticum*.

The following results were obtained in the present experiments. They are all important ones to estimate the phylogenetic relationship.

(1) One of the complementary genes, Dw_1, was found in the AB genomes (probably the B genome) of Emmer wheats, while another gene, Dw_2, was proved to be present in the D genome of *Ae. squarrosa* (as well known, common wheats were formed from Emmer wheats and *Ae. squarrosa*).

(2) The species or varieties of Emmer wheats and the strains of *Ae. squarrosa* which have Dw_1 and Dw_2 genes respectively, were made clear. In Emmer wheats, *T. dicoccoides* used which is a wild species has the Dw_1 gene, but other cultivated-type species used have the dw_1 gene except for *T. orientale*. In *Ae. squarrosa*, the majority of strains used have the Dw_2 gene and a few other strains have the dw_2 gene.

(3) The distributions of three genotypes, $Dw_1Dw_1dw_2dw_2$, $dw_1dw_1Dw_2Dw_2$, and $dw_1dw_1dw_2dw_2$, in common wheats were clarified. On the other hand, through the analyses of the genotypes of synthesized hexaploid wheats, it became possible to estimate the species of Emmer wheats and the strains of *Ae. squarrosa* which might be the parental species or strains of common wheats.

A phylogenetic relationship estimated from the above experimental results is shown in Fig. 3. This figure was, of course, drawn taking the taxonomical and genetical investigations performed by other workers and besides taking the geographical distributions of wheat species or varieties into consideration.

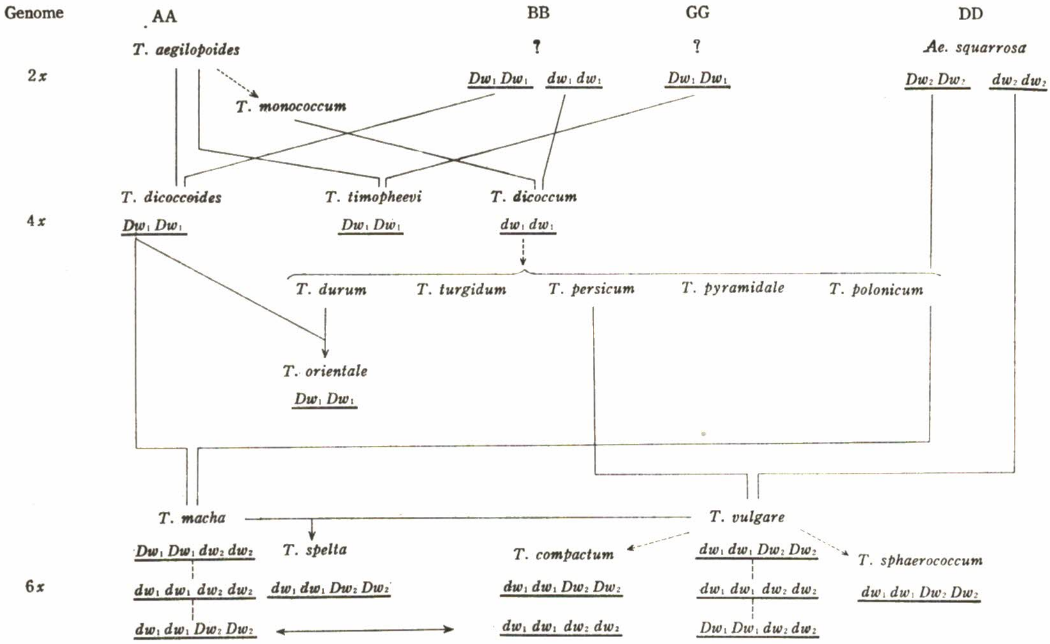

Fig. 3. Phylogenetic relationship and species differentiation in genus *Triticum* considered from the genotypes for dwarfness

—— Hybrid formation ······ Mutation ═══ Amphidiploid formation

1. Differentiation of Einkorn wheat

There are two species in Einkorn wheat, *T. aegilopoides* of wild type and *T. monococcum* of cultivated type. The most remarkable difference between both species is that in the fragility of rachis. Namely, these two species have fragile and tough rachises, respectively. The fragility is controlled by a single dominant gene (Kihara 1944). *T. monococcum* is considered to have differenitated from *T. aegilopoides* progressively by mutations and through selections. Therefore, the existence of some intermediate types has been confirmed.

2. Origin and differentiation of Emmer wheat

Since Kihara (1934) showed that Emmer wheats (AABB) originated from the hybridization between Einkorn wheat (AA) and an unknown plant having B genome, many discussions have been presented as to the unknown plant. Recently, Tanaka (1956), Sears (1956), Sarker and Stebbins (1956) and Riley et al. (1958) suggested that the S-group genomes of Sitopsis section of *Aegilops* may be the donor of the B genome. In fact, there is a considerable possibility that the B genome differentiated from the S genome.

Considering the result of the monosomic analysis performed by Hurd and McGinnis (1958), it may be possible to say that the Dw_1 or dw_1 genes are present in the B genome. If it is ture, it is considered that the S genome may have the Dw_1 or dw_1 genes.

Another important problem is which of wild-type *T. aegilopoides* and cultivated-type *T. monococcum* contributed to the origination of Emmer wheats. As seen in Table 13, except for *T. timopheevi*, the Dw_1 gene is present only in *T. dicoccoides* of wild type and *T. orientale* of cultivated type, and other Emmer wheats of cultivated type have the recessive gene, dw_1. It seems adequate to say, therefore, that Emmer wheats originated from plural parental combinations. Both the A genomes of *T. aegilopoides* and *T. monococcum* might have been independently introduced to Emmer wheats. It has been repeatedly described that the original type of Emmer wheats is *T. dicoccoides* which is a wild-type species, and that *T. dicoccum* is an intermediate-type species between such a wild-type species and many other cultivated-type Emmer wheats (Schiemann 1932 and others). However, from the fact that the dominant and recessive genes for the dwarfness are separately present in wild- and cultivated-type Emmer wheats respectively, except for *T. orientale*, it seems yet appropriate to believe the plural origins of Emmer wheats, because such a complementary gene as Dw_1 would not receive any natural selection when it exists alone. Therefore, *T. dicoccoides* of wild type might have originated from *T. aegilopoides* of wild type and a BB plant, and other Emmer wheats of cultivated type from *T. monococcum* of cultivated type and a BB plant. It is further presumed that the former received the Dw_1 gene and the latters the dw_1 gene from BB plants.

T. orientale has the Dw_1 gene, although it is a cultivated-type species. From the following evidences, it seems possible to conclude that this species was derived from a certain hybrid between *T. dicoccoides* and a cultivated-type Emmer wheat.

(1) Percival (1921) distinguished *T. orientale* from other cultivated species of Emmer wheats. Namely, he considered that *T. dicoccum* and *T. orientale* differentiated from *T. dicoccoides*, while other cultivated-type Emmer wheats came from *T. dicoccum*.

(2) *T. orientale* has some characteristics resembling *T. durum*, but it rather resembles *T. dicoccoides* as to the kernel characters and some other points.

(3) Percival (1921) considered that *T. dicoccoides fulvovillosum* was derived from the hybrid progeny of *T. dicoccoides* and *T. durum*. The author collected plants which were presumed to have originated from the above two species, in the habitat of *T. dicoccoides* (Yamashita and Tanaka 1960).

(4) This species can be found only in Asia Minor and some districts in Iran. Near by these distributing districts, *T. dicoccoides* is considered to have originated (from Hosono 1954).

Therefore, it may be reasonable to presume that *T. orientale* was originated from the hybrid between *T. dicoccoides* and *T. durum*, and that the Dw_1 gene was introduced from the former.

Although the differentiation among other cultivated-type Emmer wheats, *T. durum*, *T. turgidum*, *T. pyramidale*, *T. persicum*, and *T. polonicum*, can not be discussed from the genotype for the present dwarfness, these species probably would have differentiated from *T. dicoccum*.

As to *T. timopheevi*, it was proved that the Dw_1 gene is present in this species, and therefore this species might have relation to *T. dicoccoides* phylogenetically.

3. Origin and differentiation of Dinkel wheat

The distribution of the complementary dwarf genes in Dinkel wheats was investigated in the present study and the results as shown in Table 17 were obtained.

In *T. vulgare*, the genotypes of most varieties were $dw_1dw_1Dw_2Dw_2$ and those of some varieties were $dw_1dw_1dw_2dw_2$. But there were two varieies which had the $Dw_1D_1dw_2dw_2$ genotype, so far as the varieties used in the present study are concerned. A similar relationship was observed in *T. compactum*, but no variety with the $Dw_1Dw_1dw_2dw_2$ genotype was found. On the other hand, only the $dw_1dw_1Dw_2Dw_2$ genotype was found in *T. spelta*. *T. shaerococcum* studied had the same genotype. In T. macha, both the $dw_1dw_1Dw_2Dw_2$ and $dw_1dw_1dw_2dw_2$ genotypes were recognized. Besides, if the "semi-lethal" of Sachs (1953) is the same one with the present dwarf character, the $Dw_1Dw_1dw_2dw_2$ genotype must be present in this species.

As mentioned above, the Dw_1 and dw_1 genes are present in wild-type and cultivated-type Emmer wheats respectively, while the Dw_2 and dw_2 genes are found in *Ae. squarrosa* frequently and infrequently respectively.

Taking the distributions of these genes in *Triticum* species and *Ae. squarrosa* into consideration, and from other genetical and taxonomical evidences, Dinkel wheats can be divided phylogenetically into two groups, *T. macha* group (*macha* and *spelta*) and *T. vulgare* group (*vulgare*, *compactum* and *sphaerococcum*).

It can be recognized that *T. macha* has relation to *T. dicoccoides* as to the

Table 17. Distribution of genotypes for the dwarfness in Dinkel wheats

Species	Genotypes		
	$Dw_1Dw_1dw_2dw_2$	$dw_1dw_1dw_2dw_2$	$dw_1dw_1Dw_2Dw_2$
T. vulgare	Ceres Nōrin 3	*erythroleucon* No. 1 *graecum* No. 1 *lutescens* No. 1 (*hohenheim*)	*erythrospermum* No. 1 *alborubrum* No. 1 *albidum* No. 1 *ferrugineum* No. 1 *lutescens* No. 2 Thatcher Timstein Chinese Spring No.1 and 2
T. spelta			*duhamelianum* No. 1 *vulpinum* No. 1 *arduini* No. 1
T. compactum		*icternum* No. 1 *fetisowii* No. 1	*humboldti* No. 1 WSC KUSE No. 3063 KUSE No. 3065
T. sphaerococcum			*rubiginosum* No. 1
T. macha		*sub-letschumicum* No. 2 *palaeo-imereticum* No. 1 and 2	*sub-letschumicum* No. 1

morphological and physiological characters. Namely, *T. macha* has fragile rachises and hulled seeds, and is of prostrate type and of winter habit. This winter habit is an exceptional character in Dinkel wheats. Besides, the fragile rachises and the hulled seeds are observed only in *T. spelta*, and never in other Dinkel wheats. These characteristics of *T. macha* are all found in *T. dicoccoides*. It is generally approved that *T. macha* resembles *T. spelta* except for a few characters. Dekaprelevich and Menabde (1932) considered that *T. spelta* had been derived from *T. macha*. Kihara and his co-workers showed that the amphiploid between *T. dicoccoides* and *Ae. squarrosa* much resembled *T. spelta* morphologically (Kihara and Lilienfeld 1949, Kihara 1949 and Kihara et al. 1950). *T. macha* is found only in Caucasus, the habitat of *T. dicoccoides*.

It can be estimated, therefore, that *T. macha* originated from the hybrid formation between *T. dicoccoides* and *Ae. squarrosa*. As the synthesized hexaploid wheat from these two species has the genotype of $Dw_1Dw_1dw_2dw_2$, *T. macha* first originated from them must have had this genotype. It can be considered that *T. macha* with the $dw_1dw_1dw_2dw_2$ and $dw_1dw_1Dw_2Dw_2$ genotypes appeared afterwards by the mutations, in the direction of $Dw_1Dw_1dw_2dw_2 \rightarrow dw_1dw_1dw_2dw_2 \rightarrow dw_1dw_1Dw_2Dw_2$. It is also possible to presume that the $dw_1dw_1Dw_2Dw_2$ type *T. macha* might have originated from the natural hybrid between $dw_1dw_1dw_2dw_2$ type *T. macha* and $dw_1dw_1Dw_2Dw_2$ type hexaploid wheat, from the viewpoint that various spike densities from lax to dense are observed in *T. macha* (Dekaprelevich and Menabde 1932). On the other hand, the only one main difference between *T. vulgare* and *T. compactum* is generally considered to be in spike density. In Caucasus, considerably rich variations are observed in *T. compactum* (Vavilov 1935). Therefore, it may not be unreasonable to presume that *T. compactum* received the *compactum* gene from *T. macha,* while *T. macha* received the Dw_2 gene and also the lax-spiked gene from *T. vulgare,* in Caucasus. Furthermore, this presumed process may have relation to the origin of *T. spelta.*

At any rate, as in the presumed process, the $dw_1dw_1dw_2dw_2$ type plant must have acted an important role as a bridge between the $Dw_1Dw_1dw_2dw_2$ and $dw_1dw_1Dw_2Dw_2$ types. The homozygous double recessive genotype will be important also in the breeding works of wheats.

Concerning *T. vulgare* group, on the other hand, most *T. vulgare* and *T. compactum* have the genotype of $dw_1dw_1Dw_2Dw_2$. *T. sphaerococcum* used has also the same genotype. Since most of cultivated-type Emmer wheats have the dw_1 gene and most strains of *Ae. squarrosa* have the Dw_2 gene, it is highly probable that cultivated-type Dinkel wheats originated from a cultivated-type Emmer wheat and *Ae. squarrosa* with the Dw_2 gene. Besides, as the cultivated-type hexaploid wheats have naked seeds, the parental tetraploid wheat would be either *T. durum* or *T. turgidum* or *T. persicum* which are all naked.

The synthesized hexaploid wheat from *T. persicum* and *Ae. squarrosa* more resembles *T. vulgare* morphologically than those from other combinations (Kihara et al. 1950). Furthermore, the frequency of producing unreduced gamates in the triploid hybrid between *T. persicum* and *Ae. squarrosa* is higher than in those from other combinations (Tanaka 1959). Therefore, that *T. persicum* was the parantal Emmer wheat of the *vulgare* group has the highest possibility, as McFadden and Sears (1947) and Kihara et al. (1950) stated.

T. persicum is distributed only in Caucasus, especially in Armenia, and is coexisting with *T. macha.* But *T. vulgare* newly produced from *T. persicum* and *Ae. squarrosa* must have been isolated from *T. macha* by the isolation mechanism of the complementary dwarf genes, since the *vulgare* plant must have had the $dw_1dw_1Dw_2Dw_2$ genotype.

It can be considered that the $dw_1dw_1dw_2dw_2$ type in *T. vulgare* was produced by the mutation of the Dw_2 gene to dw_2. The rare $Dw_1Dw_1dw_2dw_2$ type might have been produced by the dominant mutation from dw_1 to Dw_1, or the dominant Dw_1 gene might have been introduced from *T. macha. T. compactum* and *T. sphaerococcum* would have been derived from *T. vulgare* in the course of the spreading of this original species.

Based on the results obtained in the present study and from the above considerations and discussions, the phylogenetical relationship of wheats as shown in Fig. 3 was estimated. The main conclusions are that (1) semi-wild-type and cultivated-type Emmer wheats have different origins one another, and (2) wild-type and cultivated-type Dinkel wheats also originated through different courses one another, provided that *T. macha* and *T. vulgare* are the respective original species.

Summary

The F_1 plants from *T. spelta duhamelianum* or *T. vulgare erythrospermum* × ABD No. 1 (amphidiploid between *T. dicoccoides spotaneo-nigrum* and *Ae. squarrosa typica* No. 2) showed a typical dwarf character. In the present study, gene analyses were performed on the dwarfness, and the genetic behavior, the origin of the dwarf genes, and the distribution of these genes in wheats and the relative species, *Ae. squarrosa*, were investigated, in order to clarify the phylogenetical relationship in genus *Triticum*. The results obtained were reported in the present paper, and some discussions were made.

1. Total 32 strains belonging to 26 varieties of wheat species and 12 strains of artificially synthesized hexaploids were used.
2. The F_1 plants from ABD No. 1 × *T. spelta duhamelianum* or *T. vulgare erythrospermum* were all semi-lethal dwarf plants.
3. In the F_2, dwarf and normal plants segregated in a ratio close to 1.6 : 1. All the normal F_2 plants bred true, while all the dwarf F_2 plants showed segregations, but with three different ratios. There was no dwarf plant which bred true.
4. Dwarf and normal plants were obtained in 1 : 1 ratio from the F_1 × *T. spelta duhamelianum*, but they segregated in a distorted ratio of about 2.7 : 1 in the reciprocal cross.
5. From the above results, it was determined that the dwarf character is controlled by two complementary dwarf genes, Dw_1 and Dw_2, which make plants dwarf when they co-exist. Namely, the genotype of ABD No. 1 is $Dw_1Dw_1dw_2dw_2$ and that of *T. spelta duhamelianum* or *T. vulgare erythrospermum* is $dw_1dw_1Dw_2Dw_2$. Thus, the F_1 plants have the $Dw_1dw_1Dw_2dw_2$ genotype.
6. It was assumed from the data in BF_1 that a competitive fertilization occurs between the Dw_1-carrying pollen and the dw_1-carrying pollen, giving a ratio of 2.7 : 1. Besides, it was considered that the $Dw_1Dw_1Dw_2Dw_2$ genotype makes embryos completely lethal, because there was no dwarf plant which bred true. From these assumption and consideration, the expected segregation ratio for dwarfs vs. normals was calculated to be 1.6 : 1. It was proved that the experimental results well fit to

this expected ratio.

7. Using ABD No. 1 and *T. spelta duhamelianum* (or in some cases *T. vulgare erythrospermum*) as the tester plants, the genotypes for the dwarfness of many Dinkel wheats and artificially synthesized hexaploid wheats were made clear.

8. Investigations on the interspecific hybrids of Emmer wheats, the intraspecific hybrids of *Ae. squarrosa*, and the artificially synthesized hexaploids proved that the Dw_1-dw_1 alleles are present in the AB genomes (probably B) of Emmer wheats and the Dw_2-dw_2 alleles in the D genome of *Ae. squarrosa*. Accordingly, Dinkel wheats must have received the former alleles from Emmer wheats and the latter from *Ae. squarrosa*.

9. From the distribution of the dwarf genes in wheats and *Ae. squarrosa*, and considering that these dwarf genes must have acted as a genetic isolation mechanism, the phylogenetical relationship in genus *Triticum* was estimated. Of course the taxonomical and genetical evidences ever published were taken into consideration.

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