COMPARATIVE GENE ANALYSIS OF COMMON WHEAT AND ITS ANCESTRAL SPECIES

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1964

CONTENTS

I. INTRODUCTION

The main aim of the present contribution, "Comparative gene analysis of common wheat and its ancestral species", was to elucidate the origin of common wheat and its later differentiation under cultivation.

There are, in fact, several different approaches for attempting this aim, which can be classified as follows:

1. Archeological approach
2. Linguistic and bibliographical approach
3. Geobotanical approach
4. Genetic approach
    a. Comparative genetics
        i. Comparative karyotype analysis
        ii. Genome analysis
        iii. Comparative gene analysis
    b. Population dynamics

The first two belong to the History of Human Culture and the last two to Botany. These different approaches should be used in coordination.

Several extensive excavations, especially those made in recent years provided important informations on the origin of wheat (Schiemann 1951), Helbaek 1952, 1959, 1961). These results have been already summarized by Nishikawa (1963). Andrews (1964) is one of those who followed the second approach, providing a new clue on the origin of spelt wheat.

The present interest, however, is concerned with the investigations carried out along the last two approaches. The first, geobotanical approach, consists of collecting variations from a wide range of habitats, investigating them by taxonomic and morphological analyses, and finally, describing the geographical attributes of the observed variations. This approach was established by de Candolle and applied for a long time as a standard method for the study of origin of cultivated plants. Vavilov (1927)

attempted to mark a further step toward the second, genetic approach and his theory on the origin of cultivated plants is known as the theory of gene centers, in which the gene center is considered to be the birthplace of a cultivated plant. However, his investigations relating, at least, to the origin of wheat and other cereals were mainly dealing with morphological and taxonomic studies of collected materials from the standpoint of geobotany, and very little work was done on their gene analysis. In this respect, the real contributions of Vavilov are of geobotanical nature.

The genetic approach deals primarily with variations of genetic material at different levels, such as genomes, chromosomes or genes. In this case, the primary object of investigation is the genetic material that determines the hereditary specificity of organisms, while its phenotypic expression, such as morphological, anatomical or physiological properties, which are subjected to selection, is considered in its importance to be secondary.

Apparently two distinct trends exist in this kind of work, one dealing with the factual data on the presently existing variations, while the other is concerned with forces and mechanisms by which a crop species was established in its present variation. In this case, processes rather than the present status are more stressed.

After the terminology of Nachtsheim (1959), the former field of genetic approach will be defined here as "Comparative genetics". In this particular field, three branches have been established, those being comparative karyotype analysis, genome analysis and comparative gene analysis.

Comparative karyotype analysis was carried out in wheat and its relatives by Kagawa (1929), Câmara (1944) and, especially extensively by Senjaninova-Korczagina (1932) and Chennaveeraiah (1960). The object of their investigations was the morphology of chromosomes or chromosome sets, but not their gene contents. Therefore, this field can be more properly

placed in the first approach, i.e., botanical.

The second field, namely, genome analysis was established by Kihara (1930) and successfully applied to many polyploid crops by later investigators. In this case, genetic homology between two given genomes is estimated by the number of bivalents formed between those two genomes at meiotic metaphase of F_1 hybrids. Genomes homologous to those of a given crop species are investigated among its relatives, thus determining the origin of individual genomes involved in that species. Three genomes of common wheat, namely, A, B and D, are now considered to have been derived from einkorn wheat, Aegilops speltoides and Ae. squarrosa, respectively (Kihara 1930, 1944, Riley, Unrau and Chapman 1958).

The third field was named as "Comparative gene analysis" by the present author. This terminology was supported by Kihara (1962). In this case, gene analysis is in parallel carried out between a given crop species and its relatives on the same genetic basis. Thus the origin of individual genes in the crop species can be elucidated. Comparative gene analysis on several important characters is expected to give a clear picture of the origin of the given species. In fact, this approach was already successfully used in barley (Takahashi 1955). In wheat, Vavilov is the pioneer in this field, though the methodological development was apparently immature at his time to realize his idea. Until the aneuploid series of common wheat, especially of monosomics, were developed by Sears (1954), critical, detailed gene analysis could not be easily carried out in common wheat, because of the presence of many duplicated loci (Tsunewaki 1962b). Comparative gene analysis thus facilitated has been given more critical meanings by the establishment of seven homoeologous groups of chromosomes (Sears 1954) and classification of all 21 chromosomes to A, B and D genomes (Sears 1954, Okamoto 1962). Nullisomic analysis (Sears 1953), monosomic analysis (Unrau 1950 and many others), chromosome substitution method (Kuspira and

Unrau 1958) and radiological study of monosomics (Tsunewaki and Heyne 1959a, b) provided useful tools for comparative gene analysis, while collection of wide variations of wheat and its relatives and production of a large number of synthesized wheats by artificial amphidiploidization (McFadden and Sears 1946, Kihara et al. 1950, Tanaka 1961) supplied it with indispensable materials.

Sears (1954) and Kuckuck (1964) carried out comparative gene analysis for species-specific characters of common wheat, clarifying the origin of species-specific genes, such as Q, C and sp, in common wheat. Mutational studies of these genes in regard to the origin of common wheat, such as those carried out by Rao and Swaminathan (1963) and Kuckuck and Peters (1964), can be placed in this category. Tanaka (1961) and Nishikawa (1963), also undertook this line of work on dwarfness and necrosis, respectively, proposing some phylogenetic relationships among various species of wheat. All those works are forerunners of the present investigation, in which distributions of individual genes controlling five important characters of wheat have been systematically studied on a much larger scale with critical methods for analysis. The results will be described hereafter and discussed in regard to the origin of individual genes found in common wheat and its implication in the origin of common wheat and its later differentiation.

A few words must be added about the second trend of genetic approach. In this case, as described above, factors and mechanisms, which caused or resulted in the present form of a crop species, are mainly concerned. This kind of work is expected to lead to elucidation of the process of evolution of a crop species. It is the field of population dynamics under cultivation. Works in this field were fruitful in the study of the origin of rice (Morishima et al. 1961, 1963). In wheat very little work has been done along this line, except those recently carried out by Zohary and Feldman(1962). At this moment, extensive researches in this field are needed for elucidating the processes involved in the evolution of wheat.

II. MATERIALS AND GENERAL METHODS

A. Materials

Three groups of wheat, namely, common wheat, emmer wheat and einkorn wheat were the object of this investigation. In common wheat, 381 varieties of Triticum aestivum L., 45 of T. compactum Host, two of T. macha Dek. et Men., five of T. spelta L. and six of T. sphaerococcum Perc. were employed. Among them 183 represent Japanese local wheat varieties, kindly supplied by Mr. T. Goto of Central Agricultural Experiment Station, Konosu; 218, collected by the members of the Kyoto University Scientific Expedition to the Karakoram and Hindukush(KUSE), were provided by Dr. M. Tanaka, Research Institute for Agricultural Plants, Faculty of Agriculture, Kyoto University. The remaining 38 varieties were obtained from various institutions in Japan, America and Europe. Ninety-four varieties of emmer wheat, belonging to nine different species, and twelve of einkorn wheat, either T. monococcum L. or T. aegilopoides Bal., were included in this investigation. All of them belong to the collection of the Samuel Rosner Chair in Agronomy, Division of Plant Science, University of Manitoba, Canada, and their specimens were kindly sent to the author by Dr. B. C. Jenkins, In addition, 14 strains of synthesized 6x wheat were employed, as listed in Table 1. Among them, three strains were synthesized by Kihara et al. (1950), eight by Tanaka (1961) and three by Sears.

Monosomic series of three common wheat varieties were employed for comparative gene analysis of common wheat and synthesized 6x wheat. They derive from T. aestivum var. Chinese Spring, var. Kharkov and var. Prelude, developed by Dr. E. R. Sears, Dr. B. C. Jenkins and Dr. R. C. McGinnis, respectively who placed them to the author's use.

B. General Methods

Comparative gene analysis

Comparative gene analysis has been carried out on five characters,

Table 1. List of synthesized 6x wheats employed in the present investigation.

Strain	Emmer parent	Ae squarrosa parent	Source
ABD- I	T. dicoccoides spont.	typica No. 2	Kihara's ABD 1
ABD- II	T. dicoccoides spont.	strangulata KUSE 2124	Tanaka's ABD 9
ABD- III	T. dicoccum Vernal	strangulata KUSE 2112	Tanaka's ABD 13
ABD- IV	T. durum Gulab	strangulata KUSE 2118	Tanaka's ABD 14
ABD- V	T. durum Gulab	meyeri KUSE 2144	Tanaka's ABD 16
ABD- VI	T. durum Golden Ball	typica Sears'	Sears
ABD- VII	T. durum Pentad	typica Sears'	Sears
ABD-VIII	T. orientale insigne	strangulata KUSE 2112	Tanaka's ABD 23
ABD- IX	T. persicum stram.	typica No. 2	Kihara's ABD 4
ABD- X	T. persicum stram.	strangulata KUSE 2135	Tanaka's ABD 11
ABD- XI	T. persicum stram.	meyeri KUSE 2144	Tanaka's ABD 22
ABD- XII	T. turgidum nigrob.	typica No. 2	Kihara's ABD 3
ABD-XIII	T. dicoccum Vernal	typica Sears'	Sears
ABD- XIV	T. persicum stram.	typica KUSE 2129	Tanaka's ABD 20

namely, progressive necrosis, waxiness, growth habit, awnedness and glume hairiness. In each case, the following principal method consisting of three steps was used:

(1) Monosomic analysis of common wheat ----- A certain number of common wheat varieties representing various types of variation were crossed to 21 lines of monosomics, and from the results obtained in the F_1 and F_2 generations the number of genes controlling a given character, their chromosomal as well as genomic location, and the mode of their interaction were determined. In parallel, diallel crosses were made in most cases among all varieties which were involved in the monosomic study. From both monosomic and conventional gene analyses, the inheritance of a given character in common wheat could be critically analyzed and the genotypes of the employed varieties were determined.

(2) Monosomic analysis of synthesized 6x wheat ----- A certain number of synthesized 6x wheats were selected so as to involve various types of emmer wheat and Ae. squarrosa as their synthetic components, and were crossed to the same monosomic series. Based on the results obtained in the F_1 and F_2 generations, genes controlling a given character of the synthetics were determined and compared with those found in common wheat. Genotypes of emmer wheat and Ae. squarrosa, the components of those synthetics were deduced from these results.

(3) Survey on the distribution of homologous genes ----- Distribution of genes, which are homologous to those identified in the limited number of varieties or strains in the above-mentioned experiments, was investigated on a large scale in common wheat, emmer wheat and Ae. squarrosa by ordinary crossing experiments or, sometimes, by simply observing their phenotypes. Einkorn wheat was in certain cases also involved. Based on these results, the distribution of a given gene in common wheat and its ancestral species was clarified.

Table 2. Frequencies of monosomics (nullisomics are included) in progenies obtained from self- and cross-pollinated monosomics.

Monosomic lines		Cross-pollinated	Self-pollinated
		%	%
Mono-	I	66.1	60.6
"	II	67.9	71.1
"	III	76.4	77.9
"	IV	73.2	63.2
"	V	70.6	69.9
"	VI	71.8	86.3
"	VII	69.6	72.4
"	VIII	75.2	68.5
"	IX	83.3	79.7
"	X	61.0	52.2
"	XI	67.2	77.1
"	XII	75.8	65.3
"	XIII	68.2	56.5
"	XIV	85.7	69.0
"	XV	67.5	75.8
"	XVI	83.7	74.0
"	XVII	83.8	71.8
"	XVIII	72.9	69.4
"	XIX	77.9	78.4
"	XX	68.4	67.1
"	XXI	67.8	70.1
Average		73.0	70.1

Monosomic analysis

Method of monosomic analysis was described in detail by Kihara and Tsunewaki (1964). In this part, therefore, only a case for a single dominant gene will be described. One may assume a recessive allele, a, in Chinese Spring and its dominant allele, A, in the variety one wants to investigate. Then F_1 between disomic Chinese Spring and that variety will show the dominant character and 3:1 simple segregation will be observed in F_2. However, if monosomics are used as female parents, two types of F_1 for each monosomic line will be produced. One has 42 chromosomes. This F_1 is a monogenic hybrid (Aa) and 3:1 segregation can be observed in F_2. The other F_1 type has 41 chromosomes. Frequency of 41-chromosome plants is more or less different among 21 monosomic lines, as shown by Tsunewaki (1963) and Tsunewaki and Heyne (1960). Their result is summarized in the second column of Table 2.

This 41-chromosome hybrid behaves just like a 42-chromosome hybrid, if the lacking chromosome is one of the 20 chromosomes which do not carry the a locus. However, if the chromosome carrying a is missing, then this F_1 has only one A, which will be expressed by the formula 0A. Such a hybrid can be obtained only once among the 21 hybrid combinations. The segregation of 0A will give rise to three types of plants, i.e., 00 (nullisomics), 0A (monosomics) and AA (disomics). Frequencies of nulli-, mono- and disomics are also dependent upon the missing chromosome, as shown by Tsunewaki (1963) and Tsunewaki and Heyne (1960). Their result is summarized in the last column of Table 2, in which frequencies of nulli- and monosomics are combined. Thus, the A gene can be located on the chromosome, whose monosomic line shows such an aberrant F_2 ratio.

Determination of chromosome number

Tsunewaki and Jenkins (1960) carried out a comparative study of various methods of root-tip preparation in screening wheat aneuploids. Their result

indicated that the cold treatment of the root-tips detached from germinating seeds is the best for an efficient screening of aneuploids. Based on their result, the following method was applied for the determination of chromosome number: Seeds were placed on wet blotting paper in a petri-dish and allowed to germinate at 20°C; two days after seeding, the primary and one of the secondary roots were collected. The detached root-tips were put in vials filled with fresh water. The vials were placed in a tray containing ice water and stored in the cold room adjusted at 0°C. The root-tips were fixed with 1:3 acetic alcohol after the 24 hour cold treatment. The Feulgen squash method was employed for cytological preparation.

III. PROGRESSIVE NECROSIS

A. Historial Review

Progressive necrosis is a hereditary trait that occurs in certain wheat hybrids, causing gradual death or weakening of plants. Among wheat breeders this type of necrosis has been known for a long time and called by different names.

In common wheat, McMillan (1936) reported first "firing" of wheat, that was accounted for three complementary genes, $\underline{F}_a$, $\underline{F}_b$ and $\underline{F}_c$. In the same year, Kostyuchenko (1936) observed a triangular relationship on "premature perishing" among three varieties, Prelude, Nowinka and Yeoman II, his explanation for that being multiple allelism in $\underline{T}$ and $\underline{L}$ loci. Later investigations, such as those carried out by Caldwell and Compton (1943) on "progressive lethal necrosis", by Heyne, Wiebe and Painter (1943) on "hybrid lethality", by Hermsen (1957) on "semi-lethality", and by Schmalz (1959) on "Subvitalität", all indicated that lethality or semi-lethality caused by necrosis is controlled by two complementary genes, which were designated as $\underline{Le}_1$ and $\underline{Le}_2$ or $\underline{A}$ and $\underline{B}$ by different authors.

In 1959, Hermsen reviewed those works, proposing a unified gene system for all types of necrosis consisting of three complementary genes, $\underline{N}_A$, $\underline{N}_B$ and $\underline{N}_D$ which in combination cause necrosis. His "three-gene hypothesis" for necrosis, however, was based merely on a theoretical consideration of previously published results without any experimental confirmation of the genetic identity between different loci which were proposed in various literatures.

Since 1960, Hermsen (1960, 1962 and 1963a, b, c) carried out quantitative investigations of necrosis with extensive materials including about 500 varieties collected from 33 countries. From those results he concluded that all types of necrosis, such as "firing", "premature perishing", "progressive lethal necrosis", "lethality", "semi-lethality" and

"Subvitalität" are under control of the same gene system. Since necrosis was found to be the chief phenotypic effect of the genes concerned, he proposed to use exclusively the basic symbol, Ne, for those genes (Hermsen 1961). The results of those further investigations led him to conclude that only two, not three, complementary genes Ne_1 and Ne_2, are involved in necrosis (Hermsen 1963c). During those investigations he found multiple alleles in both loci, namely, Ne_1^s, Ne_1^m, Ne_1^w and ne_1 in Ne_1 locus and Ne_2^s, Ne_2^{ms}, Ne_2^{wm} and ne_2 in Ne_2 locus. Different degrees of necrosis observed were accounted for those different alleles. Owing to his extensive investigation the interrelationship of various types of necrosis reported in common wheat was recognized.

Beside those works in common wheat, necrosis was found to occur in certain intergeneric hybrids between Triticum and Aegilops. For example, Sachs (1954) reported that hybrids between T. macha and Ae. squarrosa (genome formula DD) or Ae. cylindrica (CCDD) were both necrotic, indicating that one of the complementary genes is located in D genome. Roy (1955), also, observed necrotic hybrids in some crosses of species and synthetic amphidiploids of Triticum and Aegilops. Nishikawa (1960, 1962a, b) carried out a gene analysis of necrosis in crosses between emmer wheat and Ae. squarrosa, finding that there occur two types of necrosis which are controlled by two different gene systems. His type I necrosis that is controlled by Ne genes corresponds to Hermsen's necrosis. The second type of necrosis, namely, type II, is under control of Net gene system, in which two genes, Net_1 and Net_2, are involved. Those works, especially of Sachs and Nishikawa indicate that necrosis genes homologous to Ne genes of common wheat are distributed in emmer wheat and Ae. squarrosa.

All types of necrosis so far described are progressive, causing lethality or semi-lethality of plants. On the other hand, a stable necrosis is known to occur in common wheat. Sears (1954) reported that nulli-X of Chinese Spring has necrotic patches in leaves. Similar necrotic patches

were also observed in certain synthetic hexaploid wheats such as ABD No. 13 or ABD No. 20, both of them produced by Tanaka (1961). Necrosis in these cases is never progressive, plants standing well until maturity. To distinguish from this type of necrosis, Hermsen's necrosis that is the object of this chapter will be called here "progressive necrosis" after Caldwell and Compton (1943).

The author started his work on necrosis in 1958, his contributions up to date being confined to the following three points; (1) confirmation of the three-gene instead of two gene hypothesis through conventional as well as monosomic analyses of genes, (2) establishment of test varieties for the three necrosis genes, and (3) investigation on the distribution of the three genes in common wheat and its ancestors, emmer wheat and Ae. squarrosa. The results which were already published in three papers (Tsunewaki 1960, Tsunewaki and Kihara 1961, 1962) will be described in the following sections.

B. Experimental Results

1. Genetic basis of the progressive necrosis

Conventional analysis of necrosis genes

Diallel crosses were made among four varieties of common wheat, namely Kharkov, Prelude, Macha sub. and Chinese Spring. The result in regard to F_1 phenotype and F_2 segregation on necrosis is summarized in Table 3.

Unfortunately F_2 segregation could not be examined in two cross combinations, i.e. Prelude × Macha sub. and Kharkov × Macha sub., because of lethality of the F_1 hybrids. Even with such limitation, the present result clearly demonstrates that necrosis is controlled by three dominant complementary genes, which were designated as $\underline{Ne}_1$, $\underline{Ne}_2$ and $\underline{Ne}_3$ by Tsunewaki and Kihara (1961).

Based on this result, the genotypes of four varieties and their interrelationship concerning necrosis are diagrammatically shown in Fig. 1.

Table 3. F_1 phenotype and F_2 segregation of the hybrids from diallele crosses between four varieties of common wheat

Cross combination	F_1 phenotype	F_2 segregation			
		No. of plants		Ratio	x^2
		Necrotic	Normal		
Kharkov × Prelude and rec.	Necrotic (semi-lethal)	98	73	9: 7	0.1
Kharkov × Macha sub. and rec.	Necrotic (lethal)	-	-	-	-
Kharkov × Chinese Spr. and rec.	Normal	0	1,285	0: 1	0.0
Prelude × Macha sub. and rec.	Necrotic (lethal)	-	-	-	-
Prelude × Chinese Spr. and rec.	Normal	0	363	0: 1	0.0
Macha sub. × Chinese Spr. and rec.	Necrotic (semi-lethal)	135	168	27:37	0.7

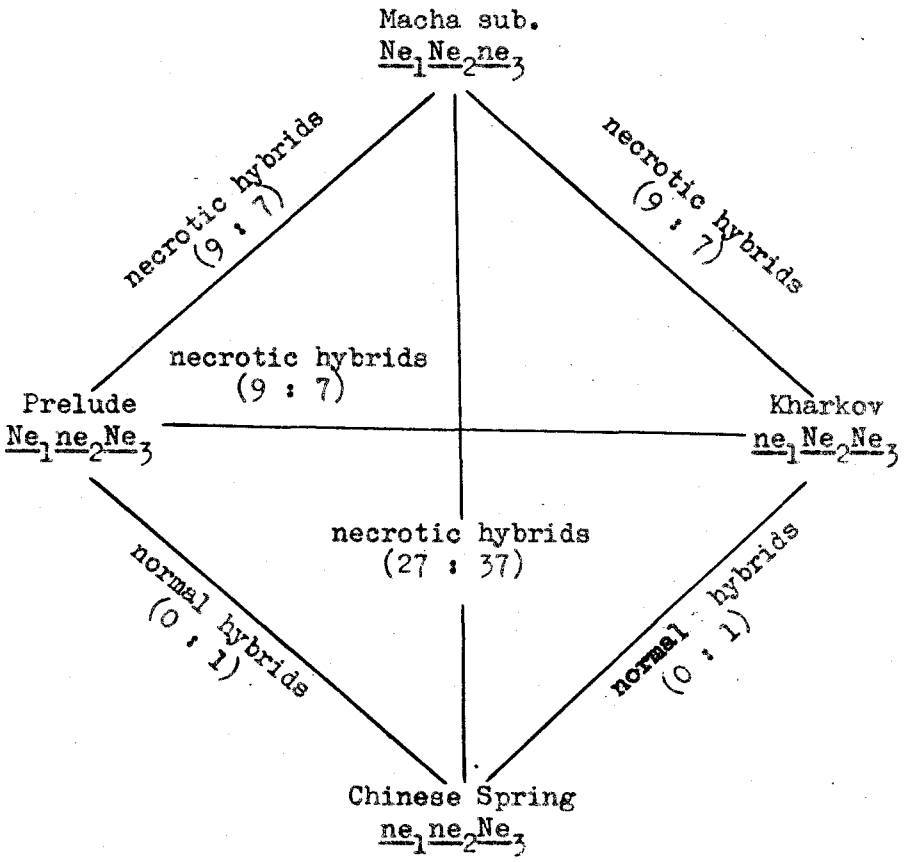


Fig. 1. Interrelationship among four varieties, Kharkov, Prelude, Macha sub. and Chinese Spring concerning necrosis. Ratio indicated in brackets is the expected F_2 ratio of necrotic to normal plants.

Monosomic analysis of the necrosis genes

(a) Location of $\underline{Ne_1}$ gene

In order to determine the location of $\underline{Ne_1}$ gene, the monosomic series of Prelude was crossed as the female with Kharkov as the male parent. Data on the phenotypic segregation of the necrotic expression in the F_1 generation are summarized in Table 4. Monosomic series of Prelude was derived from the Sears' Chinese Spring series by backcrossing. This series is in an early stage of development as the second column of Table 4 shows. Because the monosomic plants used for crosses were obtained by self-pollination, it is expected that genes on a disomic chromosome can be heterozygous or homozygous for either dominant or recessive factors. However, genes on the monosomic chromosome must be derived from Prelude.

Assuming that a Prelude chromosome carries the gene, $\underline{Ne_1}$, and another chromosome of Kharkov carries the second gene, $\underline{Ne_2}$, which together cause necrosis, the following segregation is expected in the F_1 generation of Prelude monosomics × Kharkov ($\underline{Ne_3}$ is not considered here because all three varieties, Prelude, Kharkov and Chinese Spring possess this gene in common):

(i) Non-critical monosomic lines of Prelude(♀) × Kharkov(♂)

	If ♀ is homozygous for $\underline{Ne_1}$	If ♀ is heterozygous for $\underline{Ne_1}$		If ♀ is homozygous for $\underline{ne_1}$
P generation:	$\underline{Ne_1Ne_1ne_2ne_2}$ × $\underline{ne_1ne_1Ne_2Ne_2}$	$\underline{Ne_1ne_1ne_2ne_2}$ × $\underline{ne_1ne_1Ne_2Ne_2}$		$\underline{ne_1ne_1ne_2ne_2}$ × $\underline{ne_1ne_1Ne_2Ne_2}$
F_1 generation:	$\underline{Ne_1ne_1Ne_2ne_2}$	$\underline{Ne_1ne_1Ne_2ne_2}$	$\underline{ne_1ne_1Ne_2ne_2}$	$\underline{ne_1ne_1Ne_2ne_2}$
	all necrotic	necrotic	normal	all normal

(ii) Critical monosomic line of Prelude(♀) × Kharkov(♂)

P generation: $\underline{Ne_1}$ - $\underline{ne_2ne_2}$ × $\underline{ne_1ne_1Ne_2Ne_2}$

F_1 generation: $\underline{Ne_1ne_1Ne_2ne_2}$ $\underline{ne_1}$ - $\underline{Ne_2ne_2}$

necrotic (disomic) normal (monosomic)

Table 4. Segregation of necrotic plants in the F_1 generation of Prelude monosomics × Kharkov.

F_1 lines	Generation+	No. of progenies	No. of plants		x^2 values			
			necrotic	normal	non-critical			critical
					1:0	1:1	0:1	1:3
Mono- I	2	1	15	16		.0		9.0**
"	"	3	0	68			.0	22.7**
Mono- II	3	4	84	0	.0			252.0**
Mono- III	2	6	81	0	.0			243.0**
Mono- IV	3	2	78	0	.0			234.0**
Mono- V	2	5	16	81		43.6**		3.7
Mono- VI	3	2	36	0	.0			108.0**
"	"	1	13	11		.2		10.9**
"	"	2	0	48			.0	16.0**
Mono- VII	2	2	42	0	.0			127.0**
"	2	3	16	20		.4		7.3**
Mono- VIII	2	1	6	8		.3		1.5
"	"	1	0	51			.0	17.0**
Mono- IX	3	5	125	0	.0			375.0**
Mono- X	2	2	72	0	.0			216.0**
"	"	1	27	28		.0		17.0**
Mono- XI	3	6	92	0	.0			276.0**
Mono- XII	2	2	0	71			.0	23.7**
Mono- XIII	2	1	17	0	.0			47.1**
Mono- XIV	3	2	54	0	.0			163.0**
"	"	1	8	10		.2		2.7
"	"	1	0	33			.0	11.0**
Mono- XV	2	5	112	0	.0			336.0**
Mono- XVI	4	5	108	0	.0			324.0**
Mono- XVII	2	1	16	0	.0			44.1**
"	"	2	15	16		.0		9.0**
"	"	2	0	39			.0	13.0**
Mono-XVIII	2	1	41	0	.0			123.0**
"	"	1	23	17		.9		22.5**
"	"	1	0	19			.0	5.1*
Mono- XIX	3	2	25	25		.0		16.7**
"	"	2	0	66			.0	22.0**
Mono- XX	2	4	96	0	.0			288.0**
Mono- XXI	3	4	86	0	.0			258.0**

+: Backcrossed generation of the parental monosomics.

*: Significant at the 5% level. **: Significant at the 1% level.

In the non-critical monosomic lines, whose monosomic chromosome does not carry $\underline{Ne}_1$ locus, one can expect an F_1 ratio of either 1:0, 1:1, or 0:1 for the necrotic vs. normal plants depending upon the genotype of the female parent. On the other hand, an aberrant ratio is expected for the critical monosomic line, whose single-dose chromosome carries $\underline{Ne}_1$ locus, because all disomic F_1's must be necrotic and the monosomics normal. In common wheat backcrossed offspring of a monosomic plant consists of about one part of disomic and three parts of monosomic plants, regardless which chromosome is in the monosomic condition.

Based on these considerations, the actual F_1 ratio obtained for each monosomic line was compared with the nearest ratio among the three expected for the non-critical line and the 1:3 ratio for the critical line. The x^2 values obtained are shown in Table 4.

All F_1 lines from crosses between Prelude monosomics and Kharkov, except those derived from mono-V, fitted one of the three ratios possible for a non-critical line. Two progenies, one from mono-VIII and the other from mono-XIV fitted either a critical or non-critical ratio; other progenies within these lines fitted only the non-critical ratio. This and the small size of the populations lead to the conclusion that those chromosomes do not carry genes for necrosis. The ratios obtained from lines of mono-V fitted the critical 1:3 ratio only, indicating that chromosome V of Prelude carries one of the complementary genes, i.e. $\underline{Ne}_1$, for necrosis.

(b) Location of $\underline{Ne}_2$ gene

In order to determine the location of $\underline{Ne}_2$ gene, the monosomic series of Kharkov was crossed as the female with normal Prelude as the male parent. Data on the phenotypic segregation of the necrotic expression in the F_1 generation are summarized in Table 5.

Like the above-mentioned Prelude series, Kharkov's monosomic series was also derived from the Chinese Spring series by successive backcrosses.

Table 5. Segregation of necrotic plants in the F_1 generation of Kharkov monosomics × Prelude.

F_1 lines	Generation+	No. of progenies	No. of plants		x^2 values		
			necrotic	normal	non-critical 1:0	non-critical 1:1	critical 1:3
Mono- I	7	5	85	0	.0		255.0**
Mono- II	8	5	102	0	.0		306.0**
Mono- III	8	4	88	0	.0		264.0**
Mono- IV	9	3	123	0	.0		369.0**
Mono- V	7	2	59	0	.0		177.0**
"	1	2	22	22		.0	14.7**
Mono- VI	7	4	124	1	(.0)		367.1**
Mono- VII	7	4	152	0	.0		456.0**
Mono- VIII	7	3	154	0	.0		462.0**
Mono- IX	7	3	77	0	.0		231.0**
Mono- X	7	4	119	0	.0		357.0**
Mono- XI	6	3	88	0	.0		264.0**
Mono- XII	8	4	101	0	.0		303.0**
Mono- XIII	6	3	28	120		57.2**	2.9
Mono- XIV	7	4	78	0	.0		234.0**
Mono- XV	8	3	106	0	.0		318.0**
Mono- XVI	6	4	108	0	.0		324.0**
Mono- XVII	7	3	88	1	(.0)		259.0**
Mono-XVIII	7	4	138	0	.0		414.0**
Mono- XIX	1	4	73	57		2.0	67.3**
Mono- XX	6	7	143	0	.0		429.0**
Mono- XXI	7	4	109	0	.0		327.0**

+: Backcrossed generation of the parental monosomics.

**: Significant at the 1% level.

Though the substitution backcross is much advanced in this series, as shown in the second column of Table 5, it is assumed that some genes of Chinese Spring might be still remained. If so, the same segregation ratio as was assumed in the case of Prelude monosomics × Kharkov can be expected in F_1's of the crosses between Kharkov monosomics (♀) and Prelude (♂).

Based on this consideration, the actual F_1 ratio obtained for each monosomic line was compared with the nearest ratio among the three expected for the non-critical line and the 1:3 ratio expected for the critical line. The x^2 values obtained are shown in Table 5.

All F_1 lines except those derived from mono-XIII satisfied one of the three ratios expected for a non-critical line but disagreed with the ratio for the critical line. On the other hand, the F_1 ratio obtained in the progenies of mono-XIII failed to fit any ratio for a non-critical line but satisfied the ratio expected for the critical line. These results indicate that chromosome XIII of Kharkov carries the second gene, $\underline{Ne}_2$, for necrosis.

(c) Location of $\underline{Ne}_3$ gene

In order to determine the location of $\underline{Ne}_3$ gene, the monosomic series of Chinese Spring was crossed with Macha sub. as the pollen parent. Data on the segregation of necrotic plants in the F_1 generation are summarized in Table 6.

All F_1 lines from crosses between Chinese Spring monosomics and Macha sub., except that derived from mono-XVI, satisfied one of the ratios expected for a non-critical line but rejected the ratio for the critical line. On the other hand, the F_1 ratio obtained from the line of mono-XVI fitted the critical 1:3 ratio only. These facts indicate that the third necrosis gene, $\underline{Ne}_3$, is carried on chromosome XVI of Chinese Spring.

Summary

From the results of conventional as well as monosomic analyses of

Table 6. Segregation of necrotic plants in the F_1 generation of Chinese Spring monosomics × T. Macha sub.

F_1 lines	No. of plants		x^2 values		
	necrotic	normal	non-critical 1:0	non-critical 1:1	critical 1:3
Disomic	20	0	.0	-	60.0**
Mono- I	45	0	.0	-	135.0**
Mono- II	18	11	-	1.7	21.2**
Mono- III	46	0	.0	-	138.0**
Mono- IV	29	0	.0	-	87.0**
Mono- V	20	0	.0	-	60.0**
Mono- VI	45	0	.0	-	135.0**
Mono- VII	41	0	.0	-	123.0**
Mono- VIII	33	0	.0	-	99.0**
Mono- IX	25	0	.0	-	75.0**
Mono- X	65	0	.0	-	195.0**
Mono- XI	7	0	.0	-	17.2**
Mono- XII	58	0	.0	-	174.0**
Mono- XIII	37	0	.0	-	111.0**
Mono- XIV	66	0	.0	-	198.0**
Mono- XV	33	0	.0	-	99.0**
Mono- XVI	4	22	-	12.5**	1.3
Mono- XVII	44	0	.0	-	132.0**
Mono- XVIII	32	0	.0	-	96.0**
Mono- XIX	38	1	(.0)	-	109.1**
Mono- XX	14	0	.0	-	38.1**
Mono- XXI	26	0	.0	-	78.0**

**: Significant at the 1% level.

genes, it is evident that progressive necrosis is caused by three dominant complementary genes, $\underline{Ne}_1$, $\underline{Ne}_2$ and $\underline{Ne}_3$, which are located on chromosomes V, XIII and XVI, respectively. After Okamoto (1962), chromosome V belongs to B genome, chromosome XIII to A genome and chromosome XVI to D genome. Accordingly, the three necrosis genes belong to three different genomes.

A set of the three varieties, Kharkov, Prelude and Macha sub., can be used for testing the Ne genes. Their haploid genotypes and the genes tested by them are shown in Table 7.

Any variety, which gives rise to necrotic F_1's in the cross with Kharkov, should possess, at least, $\underline{Ne}_1$ gene, while those which produce normal F_1's should contain the $\underline{ne}_1$ allele. Accordingly, Kharkov can be used as a tester for $\underline{Ne}_1$. Similarly, Prelude and Macha sub. are useful as testers for $\underline{Ne}_2$ and $\underline{Ne}_3$, respectively. Genotype of a given variety concerning necrosis can be easily determined by crossing it to those three testers.

2. Distribution of the necrosis genes in common wheat

One hundred and five varieties of common wheat were crossed to the three test varieties. Occurrence of necrosis in their F_1's is summarized in Table 8. Based on this result genotype of each variety regarding necrosis was determined that is also given in the same table.

Taking the three Ne genes into consideration, eight genotypes can be assumed for common wheat. Among them the genotype $\underline{Ne}_1\underline{Ne}_2\underline{Ne}_3$ lacking due to necrosis. Another genotype, $\underline{ne}_1\underline{ne}_2\underline{ne}_3$ will not produce any necrotic plants when crossed with all the other genotypes. Therefore, the remaining six genotypes form a necrosis hexagon, that is represented in Fig. 2.

Six out of the seven possible genotypes are represented by at least one variety. Representatives for five genotypes are also indicated in Fig. 2. Akabozu No. 1 represents the sixth genotype, $\underline{ne}_1\underline{ne}_2\underline{ne}_3$. No variety is known at present to have the genotype, $\underline{ne}_1\underline{Ne}_2\underline{ne}_3$, but it could be

Table 7. Testers for necrosis genes.

Tester	Haploid genotype			Gene tested
	Chromosome V (B genome)	Chromosome XIII (A genome)	Chromosome XVI (D genome)	
Kharkov	$\underline{ne}_1$	$\underline{Ne}_2$	$\underline{Ne}_3$	$\underline{Ne}_1$
Prelude	$\underline{Ne}_1$	$\underline{ne}_2$	$\underline{Ne}_3$	$\underline{Ne}_2$
Macha sub.	$\underline{Ne}_1$	$\underline{Ne}_2$	$\underline{ne}_3$	$\underline{Ne}_3$

Table 8. Phenotypes concerning necrosis of the F_1's between three testers and 105 varieties of common wheat.

Tested varieties	Tester (haploid genotype)			Haploid genotype of tested varieties
	Kharkov ($ne_1Ne_2Ne_3$)	Prelude ($Ne_1ne_2Ne_3$)	Macha sub. ($Ne_1Ne_2ne_3$)	
T. aestivum				
Akitazairai	-	+	+	$ne_1Ne_2Ne_3$
Blackhull	-	+	+	"
Bozu	-	+	+	"
Fulcaster	-	+	+	"
H 11	-	+	+	"
Iwate	-	+	+	"
Jones Fife	-	+	+	"
Kharkov	-	+	+	"
Oinoue	-	+	+	"
Riebesel	-	+	+	"
Sabimasari	-	+	+	"
Akabozu	+	-	+	$Ne_1ne_2Ne_3$
Akabungo	+	-	+	"
Akadaruma	+	-	+	"
Akakarashi	+	-	+	"
Akanankin	+	-	+	"
Amayoke	+	-	+	"
Bingo	+	-	+	"
Chinko	+	-	+	"
Chuchinko	+	-	+	"
Daruma	+	-	+	"
Emidashi	+	-	+	"
Itokomugi	+	-	+	"
Jujokomugi	+	-	+	"
Koshigunzairai	+	-	+	"
Kyotoakakomugi	+	-	+	"
Nowinka	+	-	+	"
Nyubai	+	-	+	"
Onakayama	+	-	+	"
Onibozu	+	-	+	"
Prelude	+	-	+	"

Shirogeshiromubo	+	-	+	$\underline{Ne_1}ne_2\underline{Ne_3}$
Shiromugi	+	-	+	"
Wakayama	+	-	+	"
Aburakomugi	-	-	+	$\underline{ne_1}\underline{ne_2}\underline{Ne_3}$
Aka	-	-	+	"
Akaboshi	-	-	+	"
Akachiku No. 1	-	-	+	"
American Banner	-	-	+	"
Asahi	-	-	+	"
Asozairai	-	-	+	"
Bankyo No. 1	-	-	+	"
Chikurin No. 36	-	-	+	"
Chinese Spring	-	-	+	"
Chinko No. 1	-	-	+	"
Chikuzen	-	-	+	"
Chuko	-	-	+	"
Ejima	-	-	+	"
<u>erythrospermum</u>	-	-	+	"
Fukoku	-	-	+	"
Fukuraku	-	-	+	"
Ichigohiderikomugi	-	-	+	"
Kagoshima	-	-	+	"
Kairyochikuzen	-	-	+	"
Karauchiwa	-	-	+	"
Kanenishiki	-	-	+	"
Koborehachikoku	-	-	+	"
Kobozu	-	-	+	"
Komugijingoro	-	-	+	"
Kozo	-	-	+	"
Marquillo	-	-	+	"
Maruhokomugi	-	-	+	"
Mubochinko	-	-	+	"
Nagasakikomugi	-	-	+	"
Nakamura	-	-	+	"
Naramisawa	-	-	+	"
Okinawazairai	-	-	+	"

Pawnee	-	-	+	$ne_1ne_2Ne_3$
S-615	-	-	+	"
Saigokuhozoroi	-	-	+	"
Seichiku	-	-	+	"
Senhoku	-	-	+	"
Senshutsuwase	-	-	+	$ne_1ne_2Ne_3$
Shibushirazu	-	-	+	"
Shiroemidashi	-	-	+	"
Sunagawadaruma No. 2	-	-	+	"
Trumbull	-	-	+	"
Yaebara	-	-	+	"
Akabozu No. 1	-	-	-	$ne_1ne_2ne_3$
T. compactum				
Akagegunbai	+	-	+	$Ne_1ne_2Ne_3$
Breadley	+	-	+	"
Hozu	+	-	+	"
Jabara	+	-	+	"
Kawabe	+	-	+	"
Nakategunbai	+	-	+	"
Akakan-Ibaragi	-	-	+	$ne_1ne_2Ne_3$
Akakomugi	-	-	+	"
Hozoroi	-	-	+	"
Ichigo-Kumamotokomugi	-	-	+	"
Ishiwari	-	-	+	"
Kinoshitakomugi	-	-	+	"
Kumamotokomugi	-	-	+	"
Mihara	-	-	+	"
Nagahokomugi	-	-	+	"
Nakateshiro	-	-	+	"
Nakatesoshu	-	-	+	"
Okugeaka	-	-	+	"
Sadabozu	-	-	+	"
Shinano No. 1	-	-	+	"
Strain No. 44	-	-	+	"
Teradabozu	-	-	+	"

T. macha				
subletschchumicum	+	+	-	$Ne_1Ne_2ne_3$
palaeoimereticum	+	-	-	$Ne_1ne_2ne_3$
T. sphaerococcum				
rotundatum	+	-	+	$Ne_1ne_2Ne_3$
T. spelta				
dubamelianum	-	-	+	$ne_1ne_2Ne_3$

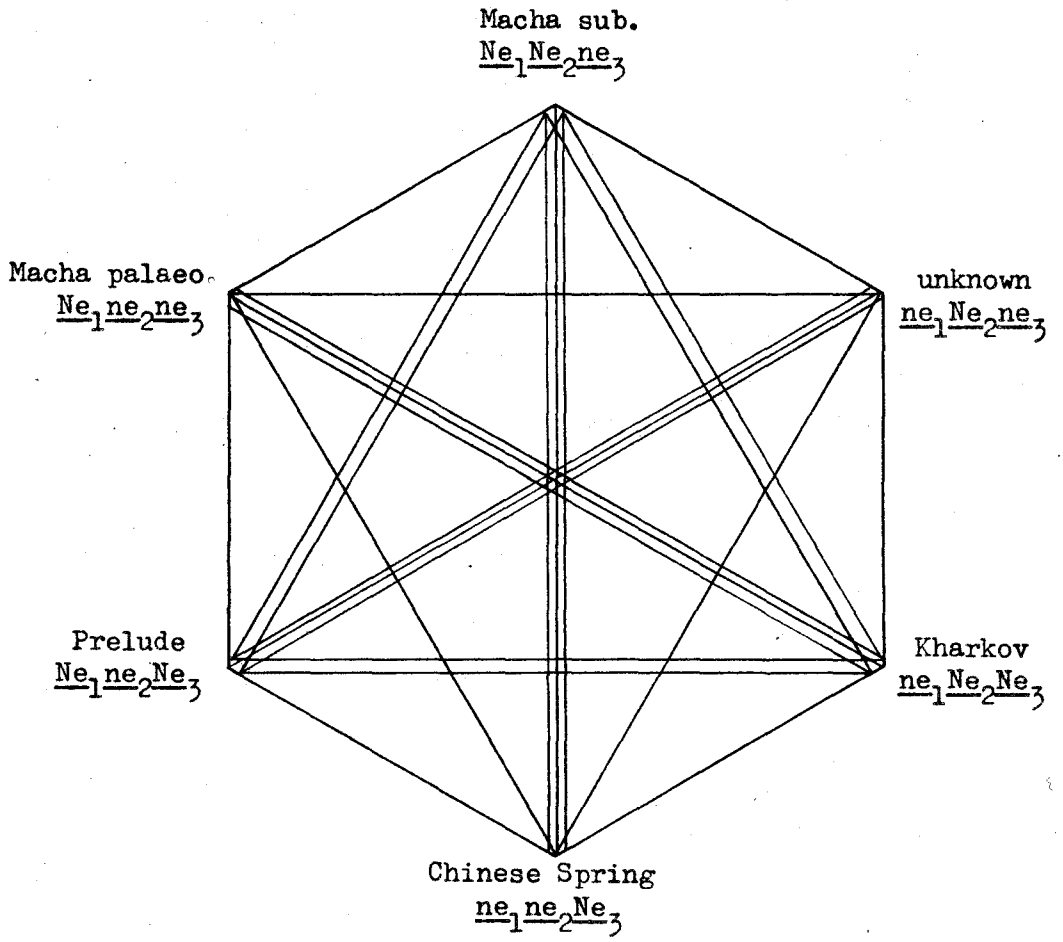


Fig. 2. Necrosis hexagon in common wheat, indicating the relationships among the six genotypes in regard to F_1 phenotype and F_2 segregation.

Single line: F_1's and F_2's normal.

Double line: necrotic F_1's and segregation of two genes in F_2's.

Triple line: necrotic F_1's and segregation of three genes in F_2's.

selected in the progeny of the cross between Macha sub. ($\underline{Ne_1Ne_2ne_3}$) and Chinese Spring ($\underline{ne_1ne_2Ne_3}$).

Frequencies of the seven possible genotypes are summarized from the data presented in the previous table, which are shown in Table 9.

A great majority of varieties were either of $\underline{ne_1ne_2Ne_3}$, $\underline{Ne_1ne_2Ne_3}$ or $\underline{ne_1Ne_2Ne_3}$. A single variety was found for each of other three genotypes, i.e. $\underline{Ne_1Ne_2ne_3}$, $\underline{Ne_1ne_2ne_3}$ and $\underline{ne_1ne_2ne_3}$. No variety was found to possess the seventh genotype, $\underline{ne_1Ne_2ne_3}$. Relative frequency of those genotypes was not significantly different between aestivum and compactum. Number of varieties tested was too small for other species to make such comparison.

Frequencies of individual alleles were calculated, which are shown in Table 10.

Concerning each allelic pair, the recessive alleles predominate in both the $\underline{Ne_1}$ and $\underline{Ne_2}$ loci, while the dominant allele is prevalent in the $\underline{Ne_3}$. The recessive allele, $\underline{ne_3}$ was found only in three varieties. Two of them belong to macha, in which no $\underline{Ne_3}$ was found. In this regard, the species, macha, is unique among the five species of common wheat.

3. Distribution of the necrosis genes in the ancestral species

In order to investigate distribution of the necrosis genes in the direct ancestors of common wheat, namely, emmer wheat and Aegilops squarrosa, twelve strains of synthesized hexaploid wheat were crossed to the three testers. The result is summarized in Table 11. Emmer and squarrosa components of the synthetics are also given in the same table.

As reported in a previous section, $\underline{Ne_1}$, $\underline{Ne_2}$ and $\underline{Ne_3}$ belong to B, A and D genome, respectively. Consequently, the first two genes found in synthetic hexaploids must have been derived from their emmer parent and the last one from squarrosa. Thus, genotypes of emmer varieties and squarrosa strains can be deduced from the genotypes of synthetics, which are summarized in Table 12. T. dicoccum var. Khapli, that produced necrotic

Table 9. Number of varieties of common wheat having each of seven possible genotypes for necrosis.

Genotypes (haploid)	Species					Total (%)
	aestivum	compactum	macha	sphaerococcum	spelta	
$\underline{ne_1}\underline{Ne_2}\underline{Ne_3}$	11	0	0	0	0	11(10.5)
$\underline{Ne_1}\underline{ne_2}\underline{Ne_3}$	23	6	0	1	0	30(28.6)
$\underline{Ne_1}\underline{Ne_2}\underline{ne_3}$	0	0	1	0	0	1(1.0)
$\underline{ne_1}\underline{ne_2}\underline{Ne_3}$	44	16	0	0	1	61(58.1)
$\underline{ne_1}\underline{Ne_2}\underline{ne_3}$	0	0	0	0	0	0(0.0)
$\underline{Ne_1}\underline{ne_2}\underline{ne_3}$	0	0	1	0	0	1(1.0)
$\underline{ne_1}\underline{ne_2}\underline{ne_3}$	1	0	0	0	0	1(1.0)
Total	79	22	2	1	1	105(100.2)

Table 10. Relative frequencies (per cent) of six alleles belonging to three loci for necrosis in common wheat

Species	Ne_1	ne_1	Ne_2	ne_2	Ne_3	ne_3
aestivum	29.1	70.9	13.9	86.1	98.7	1.3
compactum	27.3	72.7	0.0	100.0	100.0	0.0
macha, spelta, sphaerococcum	75.0	25.0	25.0	75.0	50.0	50.0
Total	30.5	69.5	11.4	88.6	97.1	2.9

Table 11. Phenotypes concerning necrosis of the F_1 hybrids between three testers and twelve strains of synthesized hexaploid wheat.

Synthetic ABD's	Synthetic components		Tester (haploid genotype)			Haploid genotype of ABD's
	Emmer wheat	Ae. squarrosa	Kharkov ($ne_1Ne_2Ne_3$)	Prelude ($Ne_1ne_2Ne_3$)	Macha sub. ($Ne_1Ne_2ne_3$)	
ABD- III	dicoccum Vernal	strangulata KUSE 2112	-	-	+	$ne_1ne_2Ne_3$
ABD- XII	turgidum nigrobarbatum	typica No. 2	-	-	+	"
ABD- VI	durum Golden Ball	" Sears'	+	-	+	$Ne_1ne_2Ne_3$
ABD-VIII	orientale insigne	strangulata KUSE 2112	+	-	+	"
ABD- X	persicum stramineum	" KUSE 2135	+	-	+	"
ABD- I	dicoccoides spont.	typica No. 2	+	-(L)	+(D)	"
ABD- II	" "	strangulata KUSE 2124	+	-	+	"
ABD- IV	durum Golden Ball	" KUSE 2118	+	-	+	"
ABD- V	" Gulab	meyeri KUSE 2144	+	-	+	"
ABD- VII	" Pentad	typica Sears'	+	-	+	"
ABD- IX	persicum stramineum	" No. 2	+(D)	-(L)	+	"
ABD- XI	" "	meyeri KUSE 2144	+	-	+	"

+: necrotic. -: non-necrotic. D: dwarf. L: lethal at the tillering stage.

F_1 hybrids when crossed to Chinese Spring ($\underline{ne_1}\underline{ne_2}\underline{Ne_3}$), is added in this table.

A majority of emmer varieties have the genotype, $\underline{Ne_1}\underline{ne_2}$, while minor fractions are either of $\underline{ne_1}\underline{ne_2}$ or $\underline{Ne_1}\underline{Ne_2}$. No variety is found to be of $\underline{ne_1}\underline{Ne_2}$. All Ae. squarrosa strains so far tested have $\underline{Ne_3}$.

C. Discussion

Two-gene vs three-gene hypothesis for necrosis

Since the two independent reports by McMillan (1936) and Kostyuchenko (1936), many papers have been published on progressive necrosis in common wheat. Reviewing those results, Hermsen (1959) proposed a three-gene hypothesis assuming that three dominant complementary genes are necessary for the expression of all types of necrosis. Later, Hermsen (1963c) discarded this three-gene hypothesis, claiming tha only two complementary genes occurred in his extensive material. In his earlier paper, Hermsen (1960) himself described a necrotic triangle among three varieties of common wheat, namely, Mendel, Mus and Macha 3, whose genotypes correspond to those of Kharkov, Prelude and Macha sub., respectively. However, he attributed the same genotype, $\underline{Ne_1}\underline{ne_2}$, to both Mus and Macha 3 in his recent paper (Hermsen 1963a). This new designation contradicts his own earlier observation that the hybrid between those two varieties was necrotic. In assuming a two-gene hypothesis he seems to have been misled for lack of a critical analysis of necrosis relationship of Macha 3 (=Macha sub.) with other varieties of genotypes $\underline{ne_1}\underline{Ne_2}$ or $\underline{ne_1}\underline{ne_2}$, according to his new designation. For examples, Chinese 166 that produced necrotic F_1's when crossed with Macha 3 ($\underline{Ne_1}\underline{ne_2}$) was designated as $\underline{ne_1}\underline{ne_2}$, and Chinese Spring that gave rise only to normal F_1's when crossed with both Prelude ($\underline{Ne_1}\underline{ne_2}$) and Kharkov ($\underline{ne_1}\underline{Ne_2}$) was considered to have the genotype $\underline{Ne_1}\underline{ne_2}$. Such contradictions seem to prove the incorrectness of the two-gene hypothesis.

Conventional as well as monosomic analyses carried out by the present

Table 12. Genotypes on necrosis of nine emmer varieties and seven strains of *Aegilops squarrosa*.

Varieties or strains	Haploid genotype
T. dicoccum Vernal	ne_1ne_2
T. turgidum nigrobarbatum	"
T. dicoccoides spontaneonigrum	Ne_1ne_2
T. durum Golden Ball	"
" Gulab	"
" Pentad	"
T. orientale insigne	"
T. persicum stramineum	"
T. dicoccum Khapli	Ne_1Ne_2
Ae. squarrosa meyeri KUSE 2144	Ne_3
" *strangulata* KUSE 2112	"
" " KUSE 2118	"
" " KUSE 2124	"
" " KUSE 2135	"
" *typica* No. 2	"
" " Sears'	"

author indicate that necrosis is caused by three complementary genes, $\underline{Ne_1}$, $\underline{Ne_2}$ and $\underline{Ne_3}$ located on chromosomes V, XIII and XVI, respectively. The location of $\underline{Ne_3}$ was later confirmed by Nishikawa (1964a). The author's result rejects Hermsen's recent hypothesis, supporting his earlier one for three complementary genes. The author's three-gene hypothesis, that is founded on the result of conventional as well as monosomic gene analyses and is in accord with the result of McMillan (1936), explains well the necrosis triangle reported by Hermsen (1960) among three varieties, Mendel, Mus and Macha 3, by assuming genotypes, $\underline{ne_1Ne_2Ne_3}$, $\underline{Ne_1ne_2Ne_3}$ and $\underline{Ne_1Ne_2ne_3}$, respectively. (Kostyuchenko's triangular relationship for Prelude-Nowinka-Yeoman II does not hold true at the present time, because the first two varieties have the same genotype, producing normal F_1's in their crosses.) Two-gene segregation observed in many hybrid combinations is, of course, ascribed to the prevalent occurrence of $\underline{Ne_3}$ gene in almost all varieties of common wheat, as was revealed by the present work. The result also confirms the prediction of Sachs (1954) that one of the complementary genes for necrosis must be in D genome and the other (actually two genes) in AB genomes. The three-gene hypothesis, furthermore, explains why necrosis has never been found in hybrids of emmer varieties, in which both $\underline{Ne_1}$ and $\underline{Ne_2}$ are present (Tsunewaki and Kihara 1962, Hermsen 1963a, Nishikawa 1964a); it is simply due to the absence of $\underline{Ne_3}$ gene. On the contrary, all those points remain unexplainable on the basis of the Hermsen's recent two-gene hypothesis.

Distribution of necrosis genes and the consideration on the origin of common wheat

As to the distribution of necrosis genes, the present author examined 105 varieties of common wheat, nine varieties of emmer wheat and seven strains of Ae. squarrosa. Nishikawa (1964b) tested 32 additional varieties of emmer wheat, crossing them to the author's testers. Including his

result for those emmer varieties, relative frequencies of the three necrosis genes in common wheat and its ancestors, emmer wheat and Ae. squarrosa, are diagrammatically shown in Fig. 3.

There is a similarity in relative frequencies of Ne_3 and ne_3 alleles between common wheat and Ae. squarrosa. That is, all squarrosa strains and a great majority of common wheat varieties have Ne_3. This fact suggests that the Ae. squarrosa, which is the donor of D genome to common wheat, must have had Ne_3.

T. macha is different from all other hexaploid species in possessing the ne_3 allele. It seems, therefore, that T. macha has been derived from some other hexaploid species, and that at that time a mutation from Ne_3 to ne_3 occurred. (The same mutation might have occurred in a Japanese variety, Akabozu No. 1.) It is less likely that T. macha has been derived from hybridization between emmer wheat and an Ae. squarrosa strain that possessed ne_3, since the existence of such squarrosa strain has not been proved yet. In either case, T. macha can be considered as an isolated species among the hexaploids and seems to be outside of the main phylogenetic path of common wheat.

As reported by Tsunewaki and Nishikawa (1964), two remarkable differences are noticed in the distribution of Ne_1 and Ne_2 at the tetra- and hexaploid levels. First a great majority of emmer varieties (61%) have the genotype Ne_1ne_2, while the most prevalent gene combination in common wheat is ne_1ne_2 (58% of the all varieties). Secondly, the gene combination ne_1Ne_2 is found in about 10% of common wheats, while it does not occur in any of the examined emmer varieties.

Accepting the hypothesis that the donor of the D genome to common wheat must have had Ne_3, some wild emmer varieties of the genotype Ne_1Ne_2 can hardly be assumed to be the progenitor of common wheat, because both the F_1's and the amphidiploids between these emmer varieties and Ae.

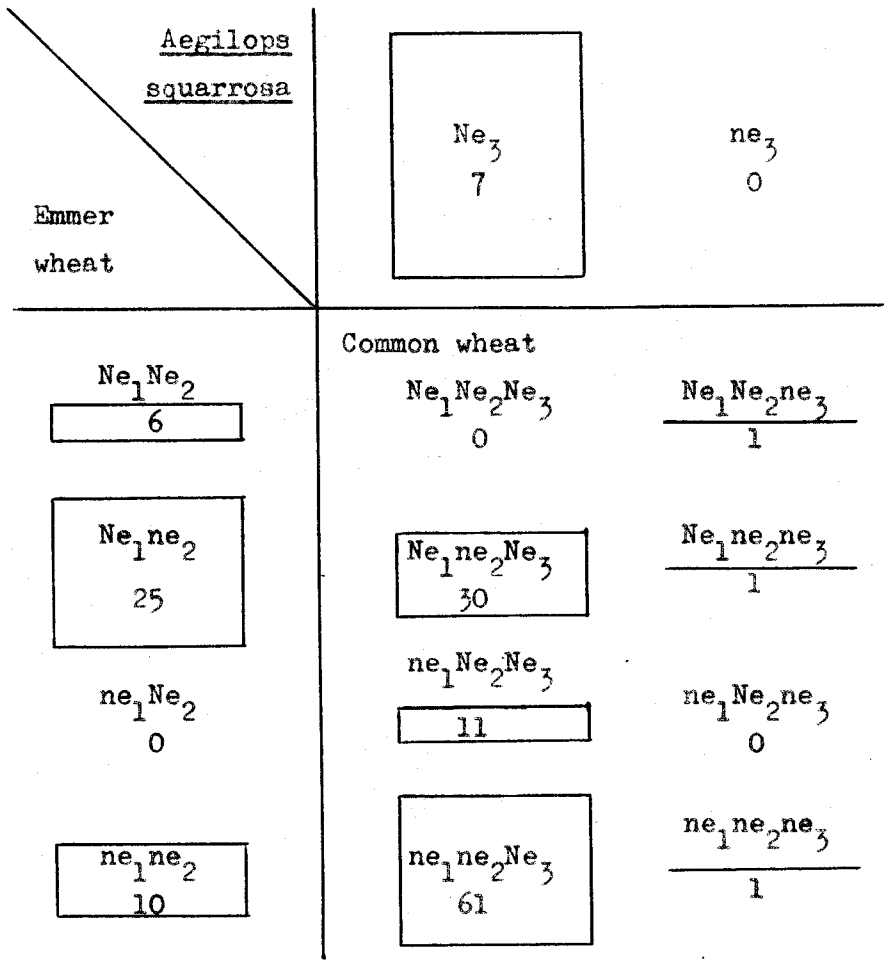


Fig. 3. Relative frequencies of different genotypes regarding necrosis in common wheat and its ancestral species. Area indicates relative frequency of each genotype in the respective group. Arabian numerals indicate the number of varieties or strains having the respective genotype.

squarrosa would be lethal due to necrosis. (After Nishikawa, 1964, five out of the six varieties of this genotype belong to wild emmer, T. dicoccoides.) On the other hand, many cultivated emmer varieties which are either $\underline{Ne_1}\underline{ne_2}$ or $\underline{ne_1}\underline{ne_2}$ can be put forward as the presumable progenitors, as proposed by Kihara and Liliénfeld (1949). The origin of $\underline{Ne_1}$, $\underline{ne_1}$ and $\underline{ne_2}$ alleles found in the present-day common wheat have to be traced back to them.

As mentioned above, no emmer varieties so far tested have the genotype $\underline{ne_1}\underline{Ne_2}$ and those of the genotype $\underline{Ne_1}\underline{Ne_2}$ could not have been the donor of the AB genomes to common wheat. These facts are in favor of the hypothesis that $\underline{Ne_2}$ of common wheat originated at the hexaploid level rather than having been introduced from emmer wheat.

The relative frequencies of $\underline{Ne_1}\underline{ne_2}$ and $\underline{ne_1}\underline{ne_2}$ gene combinations are reversed in emmer and common wheats. Since other data of the author (Tsunewaki 1962a) indicated rather frequent gene exchanges between tetra- and hexaploid wheats, this shift of the gene frequency can not be attributed to a random drift but seems to point to a special selective advantage of $\underline{ne_1}$ or disadvantage of $\underline{Ne_1}$ at the hexaploid level.

D. Conclusion

It has been confirmed that progressive necrosis in common wheat is controlled by three genes, $\underline{Ne_1}$ located on chromosome V, $\underline{Ne_2}$ on XIII and $\underline{Ne_3}$ on XVI. Eight genotypes are assumed for common wheat, among which $\underline{Ne_1}\underline{Ne_2}\underline{Ne_3}$ can not exist due to necrosis. $\underline{ne_1}\underline{ne_2}\underline{ne_3}$ does not produce any necrotic F_1's when crossed with all other genotypes. Relationships among the remaining six genotypes of common wheat concerning necrosis are represented in the diagram of Fig. 2.

Distribution of the three genes in common wheat and its ancestors, emmer wheat and Ae. squarrosa, has been investigated using Kharkov ($\underline{ne_1}\underline{Ne_2}\underline{Ne_3}$), Prelude ($\underline{Ne_1}\underline{ne_2}\underline{Ne_3}$) and Macha sub. ($\underline{Ne_1}\underline{Ne_2}\underline{ne_3}$) as test

varieties. In emmer wheat a great majority of varieties are found to have the genotype $\underline{Ne_1}\underline{ne_2}$, while minor fractions are either $\underline{ne_1}\underline{ne_2}$ or $\underline{Ne_1}\underline{Ne_2}$. All strains of Ae. squarrosa have $\underline{Ne_3}$. In common wheat, most varieties are either $\underline{ne_1}\underline{ne_2}\underline{Ne_3}$, $\underline{Ne_1}\underline{ne_2}\underline{Ne_3}$ or $\underline{ne_1}\underline{Ne_2}\underline{Ne_3}$. One variety only is found to be of each $\underline{Ne_1}\underline{Ne_2}\underline{ne_3}$, $\underline{Ne_1}\underline{ne_2}\underline{ne_3}$ and $\underline{ne_1}\underline{ne_2}\underline{ne_3}$.

From those results, the genotypes of emmer wheat, that supplied the AB genomes to common wheat, are assumed to be $\underline{Ne_1}\underline{ne_2}$ or $\underline{ne_1}\underline{ne_2}$. T. dicoccoides spontaneo-nigrum, some forms of T. dicoccum, T. turgidum, T. persicum and T. orientale, and many varieties of T. durum have these genotypes. The donor of the D genome to common wheat must have possessed $\underline{Ne_3}$. All strains of Ae. squarrosa so far tested have this allele.

The presumable hexaploid progenitor must have been of the genotype, either $\underline{Ne_1}\underline{ne_2}\underline{Ne_3}$ or $\underline{ne_1}\underline{ne_2}\underline{Ne_3}$. Some forms of T. spelta, T. sphaerococcum, T. compactum and T. aestivum have these genotypes. T. macha, that is an exception in possessing the $\underline{ne_3}$ allele, is considered to be an isolated species among the hexaploids and seems not to have contributed to the origin of common wheat.

It can be suggested that $\underline{Ne_2}$ in common wheat has been originated at the hexaploid level rather than derived from emmer wheat. Possibility of selective disadvantage of $\underline{Ne_1}$ at the hexaploid level is also suggested.

IV. WAXINESS

A. Historical Review

A waxy covering is found on stems, leaf sheaths, leaves and glumes of almost all commercial varieties of common wheat, which becomes visible in the later part of the life cycle. The color of plants with this covering appear dullish white or bluish green. Inheritance of such waxiness of foliage has been investigated by various workers.

Among emmer wheats, Miczynski (1930) crossed T. pyramidale var. recognitum (waxless) with T. durum var. affine (waxy) and found the F_1 waxless and the F_2 segregating 3 waxless:1 waxy. Chavan et al. (1956) crossed a waxless durum variety, Gaza, with two local selections (both waxy), obtaining the same result as Miczynski'.

A cross, T. dicoccoides (waxless) × T. durum (waxy), made by Kihara (1935), gave a waxless F_1 and in the F_2 waxy and waxless plants were segregated in the ratio 13:3. He assumed from this result the genotype ww II for T. dicoccoides and WW ii for T. durum. Matsumura (1950) obtained the same result in a cross between waxless T. dicoccoides and waxy T. persicum, and assigned the genotype ww IwIw to the former and WW iwiw to the latter.

In common wheat, Ayad (1952) crossed two aestivum varieties, namely Giza 139 (waxless) and Hindi 62 (waxy), and found that waxlessness is controlled by a single dominant gene. The same result was obtained in another cross, Giza 141 (waxless) × Gabo (Ayad 1953). Jensen and Driscoll (1962) crossed a waxless aestivum line with various waxy varieties of common wheat. In general, the waxless character was found to be controlled by a single dominant gene, that behaves as an epistatic inhibitor to waxy gene. Since their waxless strain was derived from a triple cross involving T. aestivum, T. polonicum and T. dicoccoides, it is strongly suspected that the waxless gene found in the hexaploid derivatives was received from T. dicocccides.

Inheritance of waxy character was also studied in pentaploid hybrids.

Watkins (1927, 1930) crossed two waxy varieties, i.e., T. turgidum Rivet and T. aestivum Swedish Iron. In the F_1, all plants became waxy, but some waxless plants were segregated in the F_2 which were all turgidum-like with fewer chromosomes than 35. By backcrossing the F_1's, it was revealed that half the egg cells contained the dominant waxy gene (W) and the remaining half the recessive waxless allele (w). From these results, he postulated the genotype W_EW_E for T. turgidum and $w_Ew_EW_DW_D$ for T. aestivum (subscripts were added by the author, E and D indicating location of the respective genes in AB and D genomes).

Allin and Vogal (1960) crossed heavily waxed T. durum (selection 396) with the monosomic series of Chinese Spring (weakly waxy). All F_1 monosomics (from mono-I to mono-XIV) were heavily waxy with the exception of mono-XIII. From this result they concluded that a gene for heavy waxiness of durum is located in chromosome XIII, being ineffective in hemizygous condition.

B. Experimental Results

1. Monosomic analysis of waxy gene in common wheat

The author examined waxiness of 220 varieties belonging to either of five common wheat species. All but one variety, T. aestivum Salmon, had waxy folliage. A further genetic investigation (Tsunewaki 1964) indicated that Salmon is deficient of the waxy gene. Based on this fact, Salmon was crossed as the male parent to 21 monosomic lines of Chinese Spring that is weakly but distinctly waxy. F_1 data on waxiness are summarized in Table 13.

F_1 plants of 19 monosomic lines were all waxy, regardless of their chromosome number. Some waxless plants were segregated in two monosomic lines, mono-XIII and XVIII. In the F_1 lines of mono-XIII, all F_1 disomics were waxy, while the monosomics were waxless. In total, about three-fourths of the F_1 population were waxless; that ratio is similar to the average frequency of monosomics. These facts indicate that a gene, W,

Table 13. Determination of waxiness in F_1 hybrids between 21 monosomic lines of Chinese Spring (waxy; ♀) and Salmon (waxless; ♂).

F_1 lines		Disomics		Monosomics		Chromosome no. unknown		Total	
		No. waxy	No. waxless	No. waxy	No. waxless	No. waxy	No. waxless	No. waxy	No. waxless
Mono-	I	4	0	2	0	12	0	18	0
"	II	1	0	5	0	33	0	39	0
"	III	-	-	6	0	10	0	16	0
"	IV	-	-	6	0	34	0	40	0
"	V	1	0	5	0	28	0	34	0
"	VI	2	0	4	0	31	0	37	0
"	VII	6	0	-	-	32	0	38	0
"	VIII	1	0	5	0	24	0	30	0
"	IX	-	-	6	0	29	0	35	0
"	X	2	0	4	0	32	0	38	0
"	XI	1	0	4	0	27	0	32	0
"	XII	4	0	2	0	28	0	34	0
"	XIII	3	0	0	3	6	22	9	25
"	XIV	-	-	6	0	27	0	33	0
"	XV	2	0	3	0	28	0	33	0
"	XVI	2	0	4	0	25	0	31	0
"	XVII	-	-	6	0	31	0	37	0
"	XVIII	2	0	2	1	10	6	14	7
"	XIX	2	0	4	0	15	0	21	0
"	XX	-	-	5	0	26	0	31	0
"	XXI	2	0	4	0	7	0	13	0

controlling waxy foliage of Chinese Spring, is located on its chromosome XIII.

In the F_1 lines of mono-XVIII, all F_1 disomics were waxy, while among three monosomics two were waxy and the remaining one was waxless; seven waxless plants being found in total. That is, there was no strict connection of monosomic condition to waxiness. This is strongly supported by the F_2 data.

Degree of waxiness of all F_1 monosomics, except waxless mono-XIII, was as weak as that of Chinese Spring.

In the F_2 generation, the following segregation was observed as shown in Table 14. Since no F_1 monosomics were found for mono-VII, F_2 data were not available for this monosomic line.

In the F_2 of disomics 3:1 segregation ratio for the waxy vs waxless plants was obtained, indicating a single dominant gene for waxy character. In all F_2 monosomic lines except that of mono-XIII, the same 3:1 ratio was obtained, while all progenies of F_1 mono-XIII were waxless. This result clearly demonstrates, in the complete agreement with the F_1 data, that a single dominant, waxy gene (W) on chromosome XIII of Chinese Spring controls waxiness of this variety. It is noteworthy that none of the waxy segregants in the F_2 was heavily waxy in comparison to Chinese Spring.

2. Monosomic analysis on waxiness of synthesized hexaploid wheat

Four strains of synthesized hexaploid wheat were used in this experiment; they are ABD-I (waxless), ABD-VI (waxless), ABD-XII (waxy) and ABD-XIII (waxless). Those four synthetics were crossed as the male parent to 21 monosomic lines of Chinese Spring (weakly waxy). Five plants from each cross were cytologically examined, selecting all monosomic F_1's and a certain number (about 20 in total) of disomics. The F_2 generation of these F_1's was further examined.

The disomic and monosomic F_1's between Chinese Spring monosomics and

Table 14. Segregation of waxiness in the F_2 generation of Chinese Spring monosomics (waxy) x Salmon (waxless).

F_2 lines	No. of progenies	No. of plants		x^2 values (3 : 1)
		waxy	waxless	
Disomic	6	154	62	1.6
Mono- I	2	25	7	.2
" II	4	79	20	1.2
" III	4	55	17	.1
" IV	3	83	35	1.4
" V	4	92	20	3.0
" VI	4	83	25	.2
" VII	0	-	-	-
" VIII	4	44	12	.4
" IX	2	78	30	.4
" X	3	89	37	1.3
" XI	3	68	14	2.7
" XII	2	49	22	1.4
" XIII	2	0	63	189.0**
" XIV	4	53	15	.3
" XV	2	67	27	.7
" XVI	3	100	30	.3
" XVII	3	58	26	1.6
" XVIII	4	50	25	2.8
" XIX	4	93	22	2.1
" XX	4	25	16	3.6
" XXI	3	85	25	.3

**:Significant at the 1% level.

ABD-XII were all waxy, while those of ABD-I, -VI and -XIII were waxless.

In the F_2 generation, no segregation of waxiness occurred in the hybrids of ABD-XII, all plants being waxy. On the other hand, the following segregation was observed in the F_2's of ABD-I, -VI and -XIII, as shown in Table 15.

In the F_2's of ABD-I, the segregation closely approached a 3:61 ratio of the waxy to waxless, rejecting a 1:15 ratio. This indicates that Chinese Spring and ABD-I differ by three allelic pairs.

In F_2 populations of both ABD-VI and -XIII segregation from disomic F_1's fit well a 1:3 ratio of waxy to waxless. F_2 ratios of all monosomic lines except mono-XX also fit this ratio. Segregation in the F_2's derived from F_1 mono-XX deviated highly significantly from the 1:3 ratio. In this population only a single plant, apparently an off-type, had waxless foliage. This result clearly indicates that a single dominant gene located on chromosome XX of ABD-VI and -XIII inhibits the expression of waxiness that is controlled by genes in A or B genome of Vernal, Golden Ball and Chinese Spring. Apparently chromosome XX of Chinese Spring carries a recessive allele of that inhibitor.

Because of the small number of F_2 plants, monosomic analysis of ABD-I was not successful in locating the genes concerned. However, the 3:61 ratio of waxy to waxless obtained in the F_2 generation of this synthetic can be reasonably interpreted as follows: Ae. squarrosa typica No. 2 carries the same inhibitor as that found in Sears' squarrosa, and T. dicoccoides spontaneo-nigrum has an epistatic inhibitor, I_W, of the waxy gene (W) in addition to the non-waxy allele, w, as reported by Kihara (1935) and Matsumura (1950).

The epistatic inhibitor of W that is present in Ae. squarrosa was first analyzed in this experiment and located on the chromosome homologous to chromosome XX of common wheat. This inhibitor will be designated here

Table 15. Segregation of waxiness in the F_2 generation of Chinese Spring monosomics × ABD-I, VI and XIII.

F_2 lines	ABD-I			ABD-VI		ABD-XIII		ABD-VI & XIII pooled		
	waxy	wax-less	x^2 (3:61)	waxy	wax-less	waxy	wax-less	waxy	wax-less	x^2 (1:3)
Disomic	8	267	1.9	205	723	105	279	310	1,002	1.3
Mono- I	0	0		25	45	0	0	25	45	4.3
" II	0	0		25	45	9	14	34	59	6.6
" III	0	1		0	5	1	5	1	10	.8
" IV	1	0		1	17	7	11	8	28	.1
" V	0	0		9	20	0	0	9	20	.6
" VI	0	3		2	8	1	7	3	15	.3
" VII	1	21		9	18	8	17	17	35	1.6
" VIII	0	0		4	11	0	1	4	12	.0
" IX	0	2		7	34	20	54	27	88	.1
" X	0	1		5	24	8	4	13	28	1.0
" XI	2	18		13	34	26	61	39	95	1.2
" XII	0	0		18	51	3	11	21	62	.0
" XIII	0	0		12	45	1	4	13	49	.5
" XIV	2	17		13	29	22	70	35	99	.1
" XV	0	0		19	58	16	34	35	92	.4
" XVI	0	0		13	36	3	9	16	45	.0
" XVII	0	13		11	33	3	15	14	48	.2
" XVIII	0	0		18	52	8	63	26	115	3.2
" XIX	0	4		4	12	8	31	12	43	.3
" XX	0	2		1	22	0	12	1	34	9.2**
" XXI	3	26		4	17	17	46	21	63	.0
Total+	17	373	.1	417	1,317	266	736	683	2,053	.0

**: Significant at the 1% level.

+: Total of disomic and all monosomic lines, except mono-XX.

as I_2-W in conformance with the article 7 of the rules for gene symbolization recommended by the International Committee of Genetic Symbols and Nomenclature (1957). Designation of the previously known inhibitor I_W will be automatically changed to I_1-W.

From the present result it is expected that an amphidiploid synthesized from T. turgidum (W i_1-W in haploid phase) and Ae. squarrosa typica No. 2 (I_2-W) must be waxless. Against this expectation the present ABD-XII is waxy. This fact suggests that I_2-W gene of Ae. squarrosa has been lost in or after the synthesis of ABD-XII.

From the results described above, the following genotypes are tentatively designated, as shown in Table 16, to two varieties of T. aestivum, four synthesized wheats, four varieties of emmer wheats and two strains of Ae. squarrosa.

W locus located on chromosome XIII will be designated as W_1, because later investigations indicated that another waxy locus (this will be designated as W_2) is carried on a chromosome of D genome. W_1 gene found in Chinese Spring is evidently weaker in its effect than that found in most emmer varieties. Therefore, this allele will be designated as W_1^c, distinguishing it by a superscript, c, from the ordinary waxy allele, W_1.

3. Investigation on waxiness of other relatives of common wheat

Waxy expression was investigated in some pure lines or varieties of wheat and its relatives. Certain hybrids were also examined for this character. The result is summarized in Table 17.

In common wheat, all varieties except Salmon were waxy. Two species of emmer wheat were found to be waxless, all the other species of this group being waxy. However, the number of varieties examined is rather small.

All seven strains of einkorn wheat were waxless. F_1 hybrids between waxless einkorn and waxy emmer varieties were produced in four different

Table 16. Genotypes on waxiness of the four synthesized 6x wheats, their synthetic components and some common wheat varieties.

Strains	Allelic series			Phenotype
	W_1 (XIII)	I_1-W (?)	I_2-W (XX)	
Synthetics				
ABD-I	w_1	I_1-W	I_2-W	waxless
ABD-VI	W_1	i_1-W	I_2-W	waxless
ABD-XII	W_1	i_1-W	i_2-W	waxy
ABD-XIII	W_1	i_1-W	I_2-W	waxless
Emmer components				
T. dicoccoides spontaneo-nigrum	w_1	I_1-W	-	waxless
T. durum Golden Ball	W_1	i_1-W	-	waxy
T. turgidum nigro-barbatum	W_1	i_1-W	-	waxy
T. dicoccum Vernal	W_1	i_1-W	-	waxy
Ae. squarrosa components				
Ae. squarrosa typica No. 2	-	-	I_2-W	waxless
" Sears'	-	-	I_2-W	waxless
Common wheat				
T. aestivum Chinese Spring	W_1^c	i_1-W	i_2-W	weakly waxy
" Salmon	w_1	i_1-W	i_2-W	waxless

Table 17. Waxy expression in common wheat, emmer wheat and their relatives, including some F_1 hybrids.

Species or strains	No. of strains	Waxiness
Common wheat		
T. aestivum	189	waxy
"	1	waxless
T. compactum	24	waxy
T. macha	2	"
T. spelta	2	"
T. sphaerococcum	2	"
Synthetic hexaploids		
ABD- I (T. dicoccoides × No. 2)		waxless
ABD- II (" × KUSE 2124)		"
ABD- III (T. dicoccum × KUSE 2112)		"
ABD- IV (T. durum × KUSE 2118)		"
ABD- V (" × KUSE 2144)		waxy
ABD- VI (" × Sears')		waxless
ABD-VIII (T. orientale × KUSE 2112)		"
ABD- X (T. persicum × KUSE 2135)		"
ABD- XII (T. turgidum × No. 2)		waxy
ABD-XIII (T. dicoccum × Sears')		waxless
ABD- XIV (T. persicum × KUSE 2129)		"
Emmer wheat		
T. dicoccoides	4	waxless
T. pyramidale	1	"
T. dicoccum	2	waxy
T. durum	5	"
T. orientale	1	"
T. persicum	2	"
T. polonicum	1	"
T. turgidum	2	"
T. timopheevi	2	waxy

Einkorn wheat		
T. monococcum	3	waxless
T. aegilopoides	4	"
Sitopsis		
Ae. aucheri	1	waxless
Ae. speltoides	3	"
"	1*	waxy
Ae. bicornis	1	waxless
Ae. sharonensis	1	"
Ae. longissima	1	"
Ae. squarrosa**		
Ae. squarrosa	many	waxless
"	few	waxy
F_1 hybrids		
T. dicoccum (waxy)×T. monococcum (waxless)		waxy
T. turgidum (waxy)×T. monococcum (waxless)		"
T. durum (waxy)×T. aegilopoides (waxless)		"
T. dicoccum (waxy)×T. aegilopoides(waxless)		"
T. aestivum (waxy)× T. dicoccum (waxy)		"
T. aestivum (waxy)×T. dicoccoides(waxless)		waxless

*:This speltoides strain was collected by BMUK.

**:Cited from Kihara and Tanaka (1958).

cross-combinations, all being waxy. This fact suggests that waxlessness of einkorn wheat is not due to the presence of an inhibitor but due to the lack of waxy gene.

Five species of Sitopsis were examined, four of them being represented by only one strain. One out of four strains of Ae. speltoides was waxy, indicating the presence of waxy gene in the speltoides genome.

After Kihara and Tanaka (1958), waxy plants of Ae. squarrosa were found in neighboring regions of Teheran, Pahlavi and Tabriz in Iran but none were found in other regions.

Eleven synthesized hexaploids were observed, all being waxless except two strains. One of them (ABD-XII) revealed by monosomic analysis that the inhibitor, I_2-W, had been lost in or after its synthesis. No critical analysis was carried out with the other waxy synthetic, ABD-V. With these exceptions, seven strains of Ae. squarrosa (all waxless) gave raise only to waxless amphidiploids when combined with waxy emmer wheats. This fact suggests that not only the two strains of Ae. squarrosa typica, which were investigated by monosomic analysis, but also other strains, such as KUSE 2129 of typica, KUSE 2112, 2118 and 2135 of strangulata and KUSE 2144 of meyeri, possess the epistatic inhibitor, I_2-W.

C. Discussion

1. Waxy genes

The present result indicates that a waxy gene of common wheat (W_1) is located on chromosome XIII and that waxy emmer varieties also possess the same gene. After Okamoto (1962) chromosome XIII belongs to A genome. Therefore, it is not surprising to find a homologue of W_1 gene in emmer wheat. In other words, the origin of W_1 gene in common wheat can be traced back to that of emmer wheat. The waxy gene in heavily waxed emmer varieties was designated by W_1 and a weaker allele found in Chinese Spring by W_1^c. Both dominate over waxless. Salmon has the recessive allele, w_1.

The results are consistent with that of Allan and Vogel (1960), who studied pentaploid hybrids between Chinese Spring monsomics and a durum wheat.

Both einkorn species, T. monococcum and T. aegilopoides, do not possess W_1 but have the w_1 allele. Therefore, the origin of W_1 found in emmer and common wheats can not be traced back to einkorn wheat. The most probable hypothesis is that w_1 mutated to W_1 at tetraploid level. T. dicoccoides spontaneo-nigrum carries w_1 allele in addition to the inhibitor I_1-W. All other varieties of this species are also waxless. Since T. dicoccoides is considered to be the progenitor of all emmer species, those facts support the present hypothesis on the origin of W_1 gene.

Extensive investigation of Ae. squarrosa undertaken by Kihara and Tanaka (1958) indicated that another waxy locus is presented in D genome. Though no critical work has been carried out with hybrids between waxy and waxless strains of Ae. squarrosa, the waxy gene present in D genome may be tentatively designated by W_2. The author's result obtained from monosomic analysis, on the other hand, clearly demonstrates that almost all strains of waxless squarrosa possess an epistatic inhibitor, I_2-W. In this case, it is uncertain whether these waxless strains possess the waxy gene, W_2, in addition to I_2-W. Monosomic analysis of the synthetics did not give any clues, because both Chinese Spring and the emmer component of the synthetics had the W_1 allele in common, that prevented the detection of segregating waxy genes in other loci. However, it is plausible to assume that most of the waxless strains possess W_2 gene. This consideration is in a good agreement with the hypothesis of Watkins (1927, 1930), who assumed two waxy loci, one in AB genomes and the other in D genome, which correspond to W_1 and W_2, respectively.

2. Epistatic inhibitors (I-W) of the waxy genes

Monosomic analysis of synthesized wheat revealed that waxlessness of Ae. squarrosa is controlled by a single dominant gene, designated as I_2-W.

This gene is located on a chromosome that is homologous to chromosome XX of common wheat. All common wheats so far tested had the recessive allele, i_2-W.

Another inhibitor, designated as I_1-W, has been known for a long time to exist in T. dicoccoides (Kihara 1935, Matsumura 1950). The present investigation confirmed this. However, its location could not be determined by monosomic analysis, because of high sterility of F_1 monosomics. T. pyramidale (Miczynski 1930) and a durum variety Gaza (Chavan et al. 1956) also possess a dominant inhibitor. This appears to be the same as I_1-W. A waxless line of T. aestivum obtained by Jensen and Driscoll (1962) from a triple cross, T. dicoccoides × T. polonicum × T. aestivum, probably received the same gene from T. dicoccoides. Two strains of an Egyptian aestivum variety, Giza, possess also a dominant inhibitor, but their origin is not known to the author (probably transferred from T. pyramidale). Besides T. dicoccoides, T. pyramidale and above-mentioned derivatives of T. durum and T. aestivum, all cultivated forms of emmer and common wheat have i_1-W. Accepting T. dicoccoides as the progenitor of all other emmer wheats, its I_1-W was transferred to T. pyramidale now under cultivation in North Africa. All other cultivated forms apparently did not receive this allele.

3. Genetic basis of waxiness and the origin of common wheat

From the results discussed above, the genetic basis of waxiness in the three groups of wheat and Ae. squarrosa became elucidated to a great extent. However, still many minor points remained for further investigations; among those location of W_2 and I_1-W loci, waxiness in the Sitopsis section of Aegilops, especially in Ae. speltoides should be found, and gene analysis of waxy vs waxless strains of Ae. squarrosa must be soon carried out.

Based on the results of the present investigation and a survey of

Table 18. Proposed genotypes for waxiness of some representatives of common wheat and its ancestral species.

Species	Variety or strain	W_1 (chr. XIII)	W_2 (D genome)	I_1-W (AB genomes)	I_2-W (chr. XX)	Phenotype
Common wheat						
T. aestivum	*erythrospermum*	W_1	W_2	i_1-W	i_2-W	heavily waxy
"	Swedish Iron	w_1	W_2	i_1-W	i_2-W	waxy
"	Chinese Spring	W_1^c	w_2	i_1-W	i_2-W	weakly waxy
"	Salmon	w_1	w_2	i_1-W	i_2-W	waxless
Emmer wheat						
T. dicoccoides	*spontaneo-nigrum*	w_1	-	I_1-W	-	waxless
T. pyramidale	*recognitum*	W_1	-	I_1-W	-	"
T. dicoccum	Vernal	W_1	-	i_1-W	-	waxy
T. durum	Golden Ball	W_1	-	i_1-W	-	"
T. turgidum	*nigro-barbatum*	W_1	-	i_1-W	-	"
Einkorn wheat						
T. monococcum	*vulgare*	w_1	-	i_1-W^*	-	waxless
T. aegilopoides	*boeoticum*	w_1	-	i_1-W^*	-	"
Ae. squarrosa	waxy strain	-	W_2	-	i_2-W	waxy
Ae. squarrosa	waxless strain	-	W_2	-	I_2-W	waxless

( ): Location of each locus.

*: Designated under the assumption that I_1-W is located in A genome.

literature, the following genotypes can be formulated, as shown in Table 18, for some representatives of common wheat and its ancestral species.

Concerning $\underline{I}_2$-$\underline{W}$ locus, all common wheat varieties possess $\underline{i}_2$-$\underline{W}$. Therefore, it is quite reasonable to assume that the donor of D genome to common wheat must have had this allele. In other words, Ae. squarrosa that contributed to the origin of common wheat must have been of the waxy type. The geographical distribution of waxy strains of Ae. squarrosa is drawn in Fig. 4 from the results of Kihara and Tanaka (1958).

As clearly shown in Fig. 4, the distribution of waxy squarrosa is limited to the mountainous region of the south-west coast of Caspian Sea. Assuming no remarkable shift in distribution of Ae. squarrosa since the formation of common wheat, its birthplace can be said to be in that region.

D. Conclusion

Results of the present investigation indicate that four loci are concerned with waxiness of common wheat; those are $\underline{W}_1$ locus on chromosome XIII of A genome, $\underline{W}_2$ in D genome (its responsible chromosome remains undetermined), $\underline{I}_1$-$\underline{W}$ in A or B genome and $\underline{I}_2$-$\underline{W}$ on chromosome XX of D genome. The former two are loci for dominant waxy genes, while the last two are for epistatic inhibitors of the waxy genes.

In common wheat, almost all varieties possess $\underline{W}_1$ or $\underline{W}_1^c$ gene and probably, $\underline{W}_2$ but lack both $\underline{I}_1$-$\underline{W}$ and $\underline{I}_2$-$\underline{W}$. Some 6x derivatives from pentaploid hybrids, however, contain $\underline{I}_1$-$\underline{W}$, that was derived from T. dicoccoides or T. pyramidale.

In emmer wheat, almost all cultivated varieties have $\underline{W}_1$ and $\underline{i}_1$-$\underline{W}$, while T. pyramidale and its derivatives have $\underline{I}_1$-$\underline{W}$ together with $\underline{W}_1$. No $\underline{w}_1$ has been found in cultivated emmer. On the other hand, wild emmer possesses $\underline{w}_1$ in addition to $\underline{I}_1$-W. Since most common wheat varieties have $\underline{W}_1$ and $\underline{i}_1$-$\underline{W}$, it can be concluded, in support of the hypothesis of Kihara and Lilienfeld (1949) on the origin of common wheat, that the donor of AB

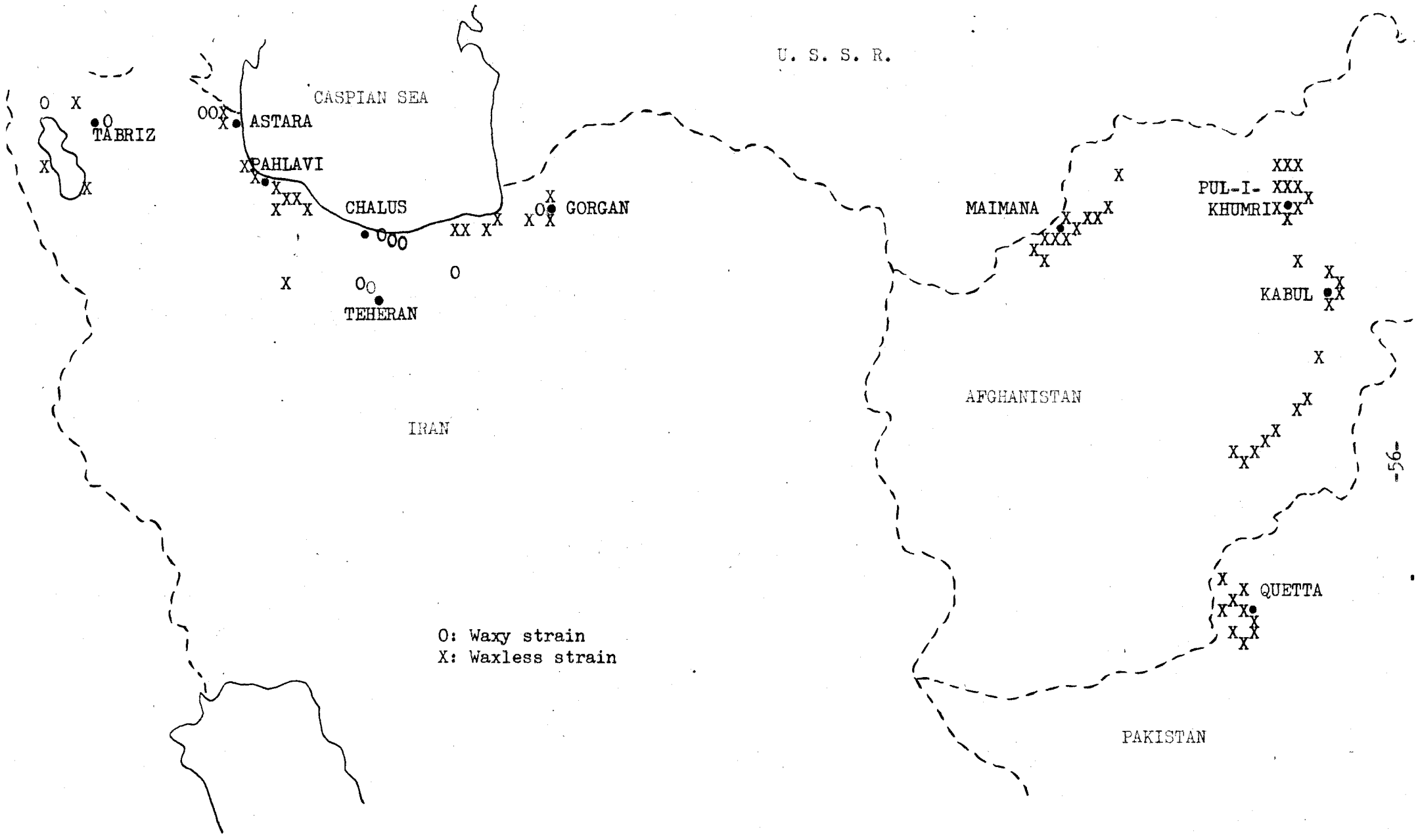


Fig. 4. Distribution of waxy strains of Ae. squarrosa.

genomes to common wheat was some cultivated emmer but not the wild one.

In Ae. squarrosa, two types are found, one of them waxy having W_2 and i_2-W and the other waxless with I_2-W and, probably, W_2. Since practically all common wheat varieties possess i_2-W but not I_2-W, the donor of D genome to common wheat must have been a waxy type.

Having those facts on one hand and the information on distribution of waxy squarrosa on the other, it can be almost definitely said that the progenitor of common wheat was formed from some waxy form of cultivated emmer and a waxy squarrosa strain in the mountainous region near to the south-west coast of Caspian Sea.

All einkorn wheats so far tested have w_1 gene. Therefore, it is most likely that the wild emmer, the progenitor of other cultivated emmer species, received this gene from einkorn. In reality, the present wild emmer possesses this gene. Mutation of w_1 to W_1 seems to have taken place in emmer wheat, probably, at an early age of its differentiation.

V. GROWTH HABIT

A. Historical Review

Since the beginning of the 20th Century, many works have been carried out on growth habit of polyploid wheats, namely, spring type vs. winter type. The results, however, were markedly different from each other, depending upon cross combinations as well as natural conditions or sowing time.

With the completion of the monosomic series in the variety Chinese Spring (Sears 1954), a genetic analysis of growth habit by means of monosomic analysis has become possible, yielding more dependable results than those obtained by the conventional methods. (The monosomic series was released by Dr. Sears for its practical use before its completion.) Therefore, the present review will be confined to the results which were obtained by the use of the monosomic series.

In crosses between 16 of the 21 Chinese Spring monosomics and a winter variety Hymar, Unrau (1950) found that chromosome IX of Hymar carries one of the two genes for winter growth habit. Location of the other gene could not be determined. Heyne and Livers (1953) reported that F_2 lines of the cross between Chinese Spring mono-XVIII and the winter variety Pawnee were resistant to winter injury. This seems to be due to the winter habit gene on chromosome XVIII of Pawnee. Kuspira and Unrau (1957) dealing with chromosome substitutions into Chinese Spring found that chromosomes XIII and XVIII of the spring variety Thatcher carry genes for winter growth habit. Knott (1959) reported that chromosome IX of the spring variety Gabo carries one of the three genes for winter habit. Morrison (1960) found that chromosomes XVIII and IX of winter varieties carry the genes responding to a vernal treatment. Furthermore, Driscoll and Jensen (1963) reported in a cross, Chinese Spring monosomics × Cornell Selection 5075aB-2B-21 (winter type), that growth habit is controlled by three pairs of genes on

chromosomes V, IX and XVIII, and, probably, by an additional gene pair on chromosome XXI. The present author also published his result on growth habit of common wheat (Tsunewaki and Jenkins 1959, 1961, Tsunewaki 1962b). Furthermore, genetic basis of this character in synthesized hexaploid wheats was studied (Tsunewaki 1962a).

Cooper (1923) designated genes controlling growth habit by S, that symbol, however, was also used for the spelta gene. The National Committee of Genetics and Breeding of the Japan Science Council (1954) recommended the symbol Sg for a gene controlling spring growth habit, while Ausemus et al. (1946) proposed the symbol Hg according to the opinion of the majority of the Committee on Nomenclature of Genetic Factors in Wheat, U.S.A. The symbol Hg, however, is more properly used for a gene controlling hairiness of glume, because the International Committee on Genetic Symbols and Nomenclature (1957) recommended the use of a common basic symbol for two or more loci having phenotypically similar effects, and the symbol H is most properly adopted for genes controlling hairiness of various plant parts such as glumes, leaves, nodes and rachis. For these reasons, Tsunewaki and Jenkins (1959, 1961) designated the loci controlling growth habit as Sg. This basic symbol will be used through out the whole thesis.

B. Experimental Results

1. Critical analysis of the growth habit in eight varieties of common wheat

Monosomic analysis

Eight varieties of Triticum aestivum or T. compactum were used in this experiment. Among those Elgin, Kharkov and Jones Fife are winter types and Chinese Spring, Prelude, Red Bobs, Red Egyptian and S-615 are spring types. Using monosomics as the female parent, each of the 21 monosomic lines of Chinese Spring was crossed with the other seven varieties, with the exception of mono-V × S-615.

The F_1 plants were grown in the greenhouse under 16 hr. illumination.

In order to facilitate the statistical analysis of the F_1 data, mono- and disomic hybrids and both parents for each series of monosomic crosses were planted according to a completely randomized design. The number of F_1 and parental plants involved is recorded in Table 19.

The heading dates of all monosomic and disomic F_1 plants were recorded and the average for a particular monosomic line was compared with the heading date of the corresponding disomic F_1 hybrid. Analysis of variance followed by a t test was applied in order to test the difference between the heading date of the disomic and each monosomic line. The 1% level was chosen for testing a mean difference, because a multirange test is not possible when subsample sizes are unequal, and more than 20 comparisons were made within a series of the monosomic crosses.

All F_1 plants produced a sufficient number of seeds for an F_2 analysis with the following exceptions: 21 monosomic lines of Chinese Spring × Red Egyptian and Chinese Spring mono-II × Kharkov and Prelude. The F_2 generation was seeded in early May in field nurseries and the plants were classified only as headed or non-headed at harvest time in early August. Segregation of the two types in each monosomic line was tested against a theoretical ratio using x^2 values. Again, the 1% level was chosen for this test, because more than 20 comparisons were made in each series of the monosomic crosses. The F_2 populations were grown according to a non-randomized design so that a certain portion of environmental effects might be confounded with the genetic effect. This is the second reason why the 1% level was chosen.

F_1 generation The average heading dates of all monosomic and disomic lines in the F_1 generation are shown in Table 20 for winter varieties and in Table 21 for spring ones. The dates are indicated by deviations in days from the heading date of the normal F_1 plants.

In crosses involving the winter varieties as the male parents, F_1

Table 19. Number of F_1 plants involved in the monosomic analysis.

F_1 lines	Chinese Spring	Hybrids between Chinese Spring monosomics and						
		Elgin	Kharkov	Jones Fife	Prelude	Red Bobs	Red Egyptian	S-615
Disomic	8	19	29	28	49	30	30	34
♀ parent	-	5	5	5	10	5	5	4
♂ parent	-	5	5	5	10	5	4	5
Mono- I	2	5	4	3	6	3	2*	2
" II	4	5	4*	4	6*	3	3*	3
" III	3	3	5	2	7	3	3*	4
" IV	2	3	4	3	9	3	5*	3
" V	4	4	5	3	5	5	2*	0*
" VI	4	4	4	4	8	4	3*	5
" VII	2	3	2	3	2	3	3*	3
" VIII	5	4	4	4	6	5	3*	6
" IX	3	5	5	5	8	3	3*	5
" X	4	2	4	3	7	4	5*	1
" XI	4	4	3	4	3	4	4*	3
" XII	3	4	4	5	7	4	5*	3
" XIII	5	5	4	3	6	2	2*	3
" XIV	2	4	3	5	6	5	3*	4
" XV	4	3	3	4	8	4	3*	2
" XVI	2	4	4	5	7	3	4*	5
" XVII	3	5	5	5	8	3	2*	4
" XVIII	3	5	5	4	9	5	5*	5
" XIX	5	5	5	4	9	3	1*	4
" XX	4	5	3	2	8	3	3*	4
" XXI	3	5	4	2	9	2	1*	3

*: F_2 generation was not grown.

Table 20. Days to heading of F_1 monosomics from crosses between Chinese Spring monosomics and three winter varieties; expressed as deviation of the heading date from that of the disomic F_1.

F_1 lines	F_1 hybrids between Chinese Spring monosomics and			
	Elgin	Kharkov	Jones Fife	Average of 3 winter var.
Disomic	105.7	102.3	97.5	101.8
♀ parent	- 8.2**	- 1.7	-10.5**	- 6.8**
♂ parent	+ ∞	+ ∞	+ ∞	+ ∞
Mono- I	+ 2.1	+ 2.2	+ 5.2**	+ 3.2
" II	+ .7	- 1.0	± .0	- .1
" III	+ 3.6	+ 1.3	- 9.5**	- 1.5
" IV	± .0	- .8	- 1.2	- .7
" V	- 1.4	- 2.0	- .5	- 1.3
" VI	- 5.2**	- 4.0	- 3.2	- 4.1
" VII	- 3.7	- 3.3	+ 2.5	- 1.5
" VIII	+ 1.3	+ 2.0	- .7	+ .9
" IX	+ 6.6**	+ 5.1**	+ 6.8**	+ 6.2**
" X	+ .5	- 1.2	± .0	- .6
" XI	+ .6	- 1.6	- 1.8	- .9
" XII	+ 1.1	+ 1.5	± .0	+ .9
" XIII	+ 2.1	+ .5	- 1.8	+ .3
" XIV	+ 3.6	+ .7	+ .5	+ 1.6
" XV	+ 5.6**	+ 2.7	+ .8	+ 3.0
" XVI	+ 3.6	+ 1.2	+ 1.5	+ 2.1
" XVII	+ 3.3	+ 2.9	+ 2.1	+ 2.8
" XVIII	+19.3**	+18.7**	+18.5**	+18.8**
" XIX	- 1.5	- 4.7**	- 2.2	- 2.8
" XX	+ 6.1**	+ 1.0	+ 3.5	+ 3.5
" XXI	- .3	- 1.5	+ 2.5	+ .2

**: Significant at the 1% level.

(+) indicates later heading and (-) indicates earlier heading of a monosomic line than that of the corresponding disomic line.

Table 21. Days to heading of Chinese Spring monosomics and their F_1 monosomics from crosses with four spring varieties; expressed as deviation of the heading date from that of the disomic F_1.

F_1 lines	Chinese Spring	F_1 hybrids between Chinese Spring monosomics and			
		Red Egyptian	S-615	Red Bobs	Prelude
Disomic	85.8	81.4	76.1	71.9	66.6
♀ parent	-	+3.4	+4.9**	+12.7**	+17.2**
♂ parent	-	+1.8	-2.1	- 1.7	- 8.0**
Mono- I	-1.3	-3.9	+1.9	+ .8	+ 1.7
" II	± .0	+3.3	- .8	+ .1	- 1.6
" III	+2.3	+1.6	+ .2	+ 2.8	+ 3.3**
" IV	+ .3	+ .6	-2.1	+ .4	- .3
" V	+3.0**	+1.1	-	+ 1.9	- .8
" VI	-2.0	-1.1	- .3	- 1.6	+ .5
" VII	+1.3	-2.1	+2.5	- 1.6	+ 3.4
" VIII	+1.1	- .1	+ .4	+ 2.5	- 2.3
" IX	+4.3**	- .1	+3.9**	- .2	+ 1.4
" X	+ .3	+2.8	+1.3	+ 2.9	- 1.2
" XI	+1.3	+1.6	- .1	+ 1.4	+ 3.0
" XII	- .4	+2.2	+1.2	+ .6	- .9
" XIII	+1.1	+2.6	+ .2	+ 6.1**	+ 5.6**
" XIV	- .3	+ .6	+1.2	+ .5	+ 1.6
" XV	+1.0	+ .3	+1.9	+ 2.1	± .0
" XVI	+1.8	+ .6	+1.7	+ 2.8	+ .7
" XVII	- .1	+ .1	+2.4	+ 1.8	+ .3
" XVIII	+6.6**	+6.2**	+2.9	+ 2.4	+ .5
" XIX	-2.0	-1.4	+1.9	+ .4	+ .7
" XX	+1.0	+ .9	+2.4	+ 1.4	+ 3.6**
" XXI	- .1	-3.4	+1.6	+ .9	+ 4.2

**: Significant at the 1% level.

(+) indicates later heading and (-) indicates earlier heading of a monosomic line than that of the corresponding disomic line.

plants monosomic for chromosomes IX and XVIII of the male parents were later to head, those monosomic for chromosome XVIII being delayed about three times as much as those monosomic for chromosome IX. Some lines monosomic for other chromosomes had effects on heading only in a certain variety.

In the crosses involving the spring varieties as male parents, F_1's monosomic for chromosomes IX, XIII and XVIII showed consistent deviations in dates of heading. The monosomic condition of chromosome IX caused delayed heading of Chinese Spring and its F_1 hybrids with S-615; that of chromosome XIII delayed heading of Red Bobs and Prelude F_1s; and that of chromosome XVIII caused delayed heading of Chinese Spring and its F_1 hybrids with Red Egyptian. Three other chromosomes had an effect only in a certain variety.

F_2 generation All plants derived from crosses between the Chinese Spring monosomics and the other spring varieties headed. Data from the F_2 segregation of crosses between the Chinese Spring monosomics and the winter varieties are presented in Table 22.

In all cases the disomic F_2 populations segregated in ratio of 10 headed to 6 non-headed plants. The monosomic F_2 line ratios have been compared to this ratio as shown with x^2 values in the corresponding column of Table 22. In all three crosses the F_2 populations derived from F_1 plants monosomic for chromosomes IX and XVIII contained a higher proportion of non-headed plants than expected and deviated significantly from the 10:6 ratio. The mono-XVIII F_2 lines contained a much higher proportion of non-headed plants than the mono-IX lines and practically all plants were non-heading.

F_2 ratios of mono-XVI, XII and XX lines for Elgin, Kharkov and Jones Fife, respectively, deviated from the 10:6 ratio. However, none of these line showed a significant deviation of the F_2 ratio from 10:6 when data for the three varieties were pooled.

Table 22. Segregation of heading types in the F_2 monosomic lines of winter varieties.

F_2 lines	Elgin		Kharkov		Jones Fife		Total		x^2 (10:6)
	No. of plants		No. of plants		No. of plants		No. of plants		
	+	-	+	-	+	-	+	-	
Disomic	723	395	789	496	735	475	2,247	1,366	.2
Mono- I	100	50	83	46	28	23	211	119	.3
" II	21	14	-	-	77	47	98	61	.1
" III	69	34	98	49	32	12	199	95	3.4
" IV	69	28	86	59	65	56	220	143	.6
" V	51	19	29	12	55	40	135	71	.8
" VI	78	41	63	29	84	56	225	126	.4
" VII	36	18	29	14	85	76	150	108	2.1
" VIII	20	8	56	48	52	34	128	90	1.3
" IX	64	74	62	92	54	87	180	253	81.0**
" X	127	61	97	73	84	33	308	167	.1
" XI	96	53	88	77	61	40	245	170	2.1
" XII	62	32	54	58	75	42	191	132	1.6
" XIII	48	28	87	62	42	28	177	118	.8
" XIV	85	44	47	28	65	31	197	103	1.3
" XV	55	35	62	46	103	61	220	142	.5
" XVI	100	32	75	44	88	54	263	130	3.3
" XVII	103	60	95	55	105	63	303	178	.1
" XVIII	5	181	1	139	0	173	6	493	800.0**
" XIX	71	24	72	48	78	58	221	130	.0
" XX	112	55	47	32	30	58	189	145	3.0
" XXI	101	50	68	50	54	43	223	143	.4

(+) and (-) indicate "headed" and "non-headed" type respectively.

**: Significant at the 1% level.

Conventional analysis

The eight varieties were crossed in diallel combinations and the F_1 plants and their parents were grown according to a randomized block design in the greenhouse under 16 hr. illumination. The number of F_1 plants studied was five for each cross combination.

The heading dates of all F_1 plants were intermediate between those of the parents. In the F_2 generation, segregation of headed and non-headed types did not occur in crosses involving only winter or only spring varieties. The data from the crosses between spring and winter varieties are summarized in Table 23.

Summary

The monosomic analysis revealed that chromosomes IX and XVIII of the three winter varieties, Elgin, Kharkov and Jones Fife had an effect for delaying heading. Chromosome IX of Chinese Spring and S-615, XIII of Prelude and Red Bobs, and XVIII of Chinese Spring and Red Egyptian also delayed heading to a less extent. No other chromosomes had a consistent effect in the various varieties or in F_1 and F_2 generations.

Those results indicate that the growth habit of common wheat is mainly controlled by genes located on chromosome IX, XIII and XVIII. The gene on chromosome XVIII of a winter variety has the most prominent effect for delaying heading followed by the gene on chromosome IX. The winter habit gene on chromosome XIII is known at present in spring varieties such as Thatcher, Prelude and Red Bobs but not in any winter varieties. From this fact, the three loci on chromosomes XVIII, IX and XIII will be designated by $\underline{Sg}_1$, $\underline{Sg}_2$ and $\underline{Sg}_3$, respectively.

The present results indicate also that the $\underline{Sg}_1$ and $\underline{Sg}_2$ loci appear to have three alleles and the $\underline{Sg}_3$ locus two of them. Concerning the $\underline{Sg}_1$ locus, all winter varieties carry a winter habit gene, two late spring varieties Chinese Spring and Red Egyptian a semi-spring habit gene and

Table 23. Actual and expected segregation of heading types in the F_2 generation of the crosses, spring varieties × winter varieties

Cross combinations	No. of plants		Expected ratios+)	x^2 values
	Headed	Non-headed		
Chinese Spring × Elgin	723	395	10:6	2.2
" × Kharkov	789	496	10:6	.7
" × Jones Fife	735	475	10:6	1.6
Red Egyptian × Elgin	207	90	11:5	.1
" × Kharkov	180	56	11:5	6.2
" × Jones Fife	268	118	11:5	.1
S-615 × Elgin	426	87	3:1	17.7**
" × Kharkov	421	67	3:1	33.1**
" × Jones Fife	421	61	3:1	39.2**
Red Bobs × Elgin	416	30	58:6	3.7
" × Kharkov	395	33	58:6	1.4
" × Jones Fife	281	28	58:6	.0
Prelude × Elgin	380	42	58:6	.2
" × Kharkov	66	5	58:6	.5
" × Jones Fife	89	13	58:6	1.4

+) "Headed" vs. "non-headed".

**: Significant at the 1% level.

the other spring varieties a typical spring habit gene; these will be designated by $\underline{sg_1}$, $\underline{Sg_1^c}$ and $\underline{Sg_1}$, respectively. The $\underline{Sg_2}$ locus also carries three genes, namely, a winter habit gene in the winter varieties, a semi-spring habit gene in two late spring varieties, Chinese Spring and S-615, and a typical spring habit gene in the other spring varieties. These genes can be designated by $\underline{sg_2}$, $\underline{Sg_2^c}$ and $\underline{Sg_2}$, respectively. The $\underline{Sg_3}$ locus carries two genes, i.e., a semi-spring habit gene in Prelude and Red Bobs and a typical spring habit gene in the other varieties; these being designated by $\underline{sg_3}$ and $\underline{Sg_3}$, respectively. In all cases dominance is in order of spring, semi-spring and winter habit, because the F_1s between early and late varieties were much more similar to the early variety in regard to their heading date.

The haploid genotypes for each of the eight varieties may then be formulated as follows:

Elgin, Kharkov and Jones Fife;	$\underline{sg_1}$	$\underline{sg_2}$	$\underline{Sg_3}$
Chinese Spring ;	$\underline{Sg_1^c}$	$\underline{Sg_2^c}$	$\underline{Sg_3}$
Red Egyptian ;	$\underline{Sg_1^c}$	$\underline{Sg_2}$	$\underline{Sg_3}$
S-615 ;	$\underline{Sg_1}$	$\underline{Sg_2^c}$	$\underline{Sg_3}$
Prelude and Red Bobs ;	$\underline{Sg_1}$	$\underline{Sg_2}$	$\underline{sg_3}$

Based on the proposed genotypes the crosses between Chinese Spring and the winter varieties would be segregating for two pairs of genes, $\underline{Sg_1^c}$, $\underline{sg_1}$ and $\underline{Sg_2^c}$, $\underline{sg_2}$. The segregation clearly fit a 10:6 ratio of headed to non-headed plants. This segregation can be explained on the assumption that plants homozygous for $\underline{sg_1}$ and those heterozygous for $\underline{sg_1}$ and homozygous for $\underline{sg_2}$ failed to head. This hypothesis is partly supported by the fact that only a few plants headed among the progenies derived from F_1 hybrids monosomic for chromosome XVIII.

In the crosses between Red Egyptian and the winter varieties, the segregation will be for the two gene pairs $\underline{Sg_1^c}$, $\underline{sg_1}$ and $\underline{Sg_2}$, $\underline{sg_2}$. These

F_2 populations segregated in an 11:5 ratio, as shown in Table 23, which can be explained by the fact that the $\underline{Sg_2}$ gene is more effective in producing spring habit than the $\underline{Sg_2^c}$ gene of Chinese Spring and that only plants homozygous for $\underline{sg_1}$ and homo- or heterozygous for $\underline{sg_2}$ and those heterozygous for $\underline{sg_1}$ and homozygous for $\underline{sg_2}$ failed to head. All plants homozygous for $\underline{Sg_1^c}$ or $\underline{Sg_2}$ gene or heterozygous for both genes headed.

In the crosses between S-615 and the winter varieties segregation occurs for two gene pairs $\underline{Sg_1}$, $\underline{sg_1}$ and $\underline{Sg_2^c}$, $\underline{sg_2}$. Only plants homozygous for $\underline{sg_1}$ gene are expected not to head. The F_2 generation should, therefore, segregate in a 12:4 or 3:1 ratio of headed to non-headed plants but it produced more headed plants than can be explained from a dihybrid segregation as shown in Table 23.

In the crosses between Red Bobs and Prelude and the winter varieties three gene pairs $\underline{Sg_1}$ $\underline{sg_1}$, $\underline{Sg_2}$ $\underline{sg_2}$ and $\underline{Sg_3}$ $\underline{sg_3}$ are segregating and in this case plants with a genotype either $\underline{sg_1}$ $\underline{sg_1}$ $\underline{sg_2}$ $\underline{sg_2}$ - - or $\underline{sg_1}$ $\underline{sg_1}$ $\underline{Sg_2}$ $\underline{sg_2}$ $\underline{sg_3}$ $\underline{sg_3}$ would fail to head. Actual F_2 data fit well this expection, segregating in 58:6 ratio of headed to non-headed plants as shown in Table 23.

Apparently, genotypes of the eight varieties proposed from the result of monosomic analysis explain well the F_2 segregation in diallel crosses with the exception of S-615 x winter varieties. In this case segregation of minor genes such as those found by Sears (1953) and Kuspira and Unrau (1957) must be considered in addition to that of three major genes.

2. Monosomic analysis of synthesized 6x wheats

In order to elucidate genetic basis of the growth habit in emmer wheat and Ae. squarrosa, four synthesized 6x wheats with different synthetic components were studied by means of monosomic analysis. The strains employed were winter type ABD-I and spring type ABD-VI, -XII and -XIII.

Each of the four synthetics was crossed as the male parent with 21 monosomic lines of Chinese Spring as the female. All F_1 plants were seeded

and grown in the greenhouse under 24 hr. illumination. The numbers of monosomic and disomic F_1 plants involved in this experiment are recorded in Table 24.

In order to facilitate the statistical analysis of the F_1 data, mono- and disomic hybrids of each series of monosomic crosses were planted according to a completely randomized design. Heading date was then recorded for individual plants. In order to test the effect of a chromosome on heading date, the average heading date of a particular monosomic line was compared with that of the corresponding disomic F_1's. Analysis of variance followed by a t test was applied to these data.

Monosomic F_1 plants of ABD-VI, -XII and -XIII were less fertile than the corresponding disomic F_1's but the majority of them produced sufficient seeds for the monosomic analysis of the F_2 generation. In contrast, F_2 monosomic analysis of ABD-I could not be satisfactorily carried out, because monosomic F_1's of this strain were almost completely sterile.

The F_2 generation was planted in the greenhouse, moved outdoors soon after germination and then grown in the field under natural conditions. The number of F_2 hybrids tested is indicated in Table 24.

The average heading dates of all monosomic and disomic lines in the F_1 generation are shown in Table 25. The heading dates of the monosomic lines are indicated by deviations in days from the dates of the corresponding disomic F_1's.

Among 20 F_1 monosomic lines of the winter type, ABD-I, mono-IX and -XVIII showed significantly later heading than the disomic. Delay of heading of mono-XVIII was much greater than that of mono-IX.

In the crosses involving ABD-XII and -XIII as male parents, both of which mature earlier than the other synthetics, F_1's monosomic for chromosome XIII showed consistently later heading than the corresponding disomic. In addition, F_1 mono-XX of ABD-XII and mono-II of ABD-XIII showed significantly delayed heading.

Table 24. Number of F_1 and F_2 hybrids involved in the monosomic analysis.

Strains	F_1's				F_2's			
	ABD-I	ABD-VI	ABD-XII	ABD-XIII	ABD-I	ABD-VI	ABD-XII	ABD-XIII
Disomic	18	26	25	23	287	932	824	384
Mono- I	5	3	2	1	0	75	30	0
" II	4	5	2	6	0	71	35	24
" III	4	1	3	3	2	5	30	6
" IV	4(1)	2	2	4	1	18	13	18
" V	4(2)	4	4	3	0	29	44	0
" VI	4	4(1)	4	3	3	10	109	8
" VII	4(1)	2	3(1)	3(1)	22	27	30	25
" VIII	4	5	4	3	0	15	42	2
" IX	5	5(1)	0	5	2	41	0	76
" X	3	2	0	4	1	30	0	12
" XI	4	3	2	3	20	47	80	87
" XII	5(3)	3	3	3	0	70	46	14
" XIII	3(1)	4	2	3(1)	0	57	17	5
" XIV	1	2	2	5	20	42	19	92
" XV	2	2	5	4	0	78	38	50
" XVI	1	3(1)	5	1	0	49	86	12
" XVII	4	3	0	3	13	44	0	18
" XVIII	3	3	3	5	0	72	72	73
" XIX	5(1)	3(1)	1	5	5	18	40	40
" XX	4	4	3	2	3	23	45	12
" XXI	2	1	4	3	30	22	119	63

( ): Number of plants having 40 instead of 41 chromosomes, seemingly doubly monosomic.

Table 25. Days to heading of the F_1 hybrids from crosses between Chinese Spring monosomics and four synthesized 6x wheats; expressed as deviation of the heading date from that of the disomic F_1.

F_1 lines	Male parents			
	ABD-I	ABD-VI	ABD-XII	ABD-XIII
Disomic	92.1	80.0	75.1	76.6
Mono- I	- 0.9	- 1.0	- 0.6	+ 2.4
" II	- 2.1	- 1.6	+ 3.4	+ 4.6**
" III	+ 1.2	+ 1.0	+ 1.4	+ 2.8
" IV	- 0.1	+ 1.0	+ 1.9	+ 1.4
" V	+ 0.7	± 0.0	+ 1.7	+ 1.1
" VI	- 1.6	- 1.3	- 1.1	+ 3.4
" VII	+ 0.9	- 1.5	- 0.8	- 0.6
" VIII	- 4.6	- 2.6	- 2.3	- 0.9
" IX	+ 6.3**	+ 3.2**	-	+ 0.2
" X	- 4.7	+ 1.5	-	- 0.3
" XI	- 3.8	+ 2.0	+ 0.4	- 0.2
" XII	+ 4.4	- 1.0	- 1.4	+ 0.1
" XIII	- 1.1	- 0.7	+ 6.4**	+ 4.1**
" XIV	+ 3.9	- 0.5	+ 1.9	+ 0.2
" XV	- 5.1	+ 2.5	+ 1.9	- 0.8
" XVI	-	- 0.7	- 0.7	+ 2.4
" XVII	+ 0.4	- 1.7	-	- 0.2
" XVIII	+36.9**	+ 5.0**	+ 1.3	- 0.8
" XIX	- 4.1	- 0.5	- 0.1	- 1.2
" XX	+ 2.4	+ 2.5	+ 3.9**	- 0.1
" XXI	- 4.1	- 2.0	+ 0.9	- 0.2

** : Significant at the 1% level.

(+) indicates later heading and (-) indicates earlier heading of a monosomic line than that of the corresponding disomic line.

In the crosses involving as male parent ABD-VI, that had the latest heading date among the three spring-type synthetics, F_1's monosomic for chromosomes IX and XVIII showed later heading. In this case, too, heading of mono-XVIII was later than that of mono-IX.

In the F_2 generation of these monosomic crosses, no segregation of winter type occurred in hybrids of ABD-VI, -XII and -XIII. On the other hand, the F_2 of Chinese Spring × ABD-I segregated 20 winter type plants among 409, indicating a 15:1 ratio for the spring vs. winter habit. This result and that from the F_1 generation indicate that winter growth habit of ABD-I is controlled by two recessive alleles on chromosomes IX and XVIII, the one on chromosome XVIII being more effective than that on chromosome IX. As the 14 chromosomes from I to XIV belong to the A or B genome and the seven chromosomes from XV to XXI to the D genome, the gene on chromosome IX is most likely responsible for the winter habit of T. dicoccoides and seems to be the same as the sg_2 allele of common wheat. The other gene on chromosome XVIII derived from Ae. squarrosa No. 2 controls winter growth habit of this squarrosa strain and apparently is the same as the sg_1 allele of common wheat.

Factorial analysis of growth habit genes in ABD-VI, -XII and -XIII was not made, because all the F_2's were spring type. However, F_1 data indicate that genes located on chromosomes IX and XVIII are responsible for late maturity of ABD-VI. From their location and function, the genes on chromosome IX and XVIII of ABD-VI seem to be the same as Sg_2^c and Sg_1^c of common wheat, respectively. In other words, the Sg_1^c allele of common wheat is also present in Sears' Ae. squarrosa strain and Sg_2^c in the spring durum variety, Golden Gall.

F_1 data, also, indicate that chromosome XIII of two early spring strains, ABD-XII and -XIII, carries a less effective spring-habit allele than that on chromosome XIII of Chinese Spring. This allele originating

from the emmer species, T. turgidum and T. dicoccum Vernal seems from its location and function to be the same as the sg_3 allele in early spring varieties of common wheat. Chromosome XIII of ABD-I and -VI and its homologues in T. dicoccoides spontaneo-nigrum and T. durum Golden Ball seem to carry the typical spring-type allele, Sg_3, because the hemizygous condition did not cause a delay of heading.

Based on those results, the following genotypes will be proposed to the four synthetic 6x wheats and their respective components as shown in Table 26.

C. Discussion

On the origin of common wheat

Growth habit of common wheat has been revealed here to be mainly controlled by genes belonging to three allelic series, Sg_1 on chromosome XVIII (D genome), Sg_2 on IX (A) and Sg_3 on XIII (A). Each of the Sg_1 and Sg_2 series has three alleles and the Sg_3 series has two; the alleles being Sg_1, Sg_1^c and sg_1, Sg_2, Sg_2^c and sg_2 and Sg_3 and sg_3 in order of dominance for each series. All winter varieties so far tested carried the typical winter habit genes, sg_1 and sg_2. The gene sg_1 was much more effective than sg_2 in delaying heading. The sg_1 gene was also found in a winter type strain of Ae. squarrosa.

In barley, Yasuda (1961) produced F_2 populations from several crosses between winter and spring varieties, and studied the frequencies of growth habit genes in their F_3 and later generations, growing them in four different localities in Japan. In this case seeding was made in the fall. In a hybrid population that was grown in the northern part, the frequency of winter habit allele was remarkably increased within a few generations, while in that grown in the southern part it was decreased. His result clearly demonstrates that the winter habit allele has under fall planting

Table 26. Genotypes for growth habit of the four synthesized 6x wheats and their synthetic components.

Strains	Loci		
	$\underline{Sg}_1$ (XVIII)	$\underline{Sg}_2$ (IX)	$\underline{Sg}_3$ (XIII)
Synthesized 6x			
ABD-I	$\underline{sg}_1$	$\underline{sg}_2$	$\underline{Sg}_3$
ABD-VI	$\underline{Sg}_1^c$	$\underline{Sg}_2^c$	$\underline{Sg}_3$
ABD-XII	$\underline{sg}_1$	$\underline{Sg}_2$	$\underline{sg}_3$
ABD-XIII	$\underline{Sg}_1^c$	$\underline{Sg}_2$	$\underline{sg}_3$
Emmer components			
T. dicoccoides spontaneo-nigrum	-	$\underline{sg}_2$	$\underline{Sg}_3$
T. durum Golden Ball	-	$\underline{Sg}_2^c$	$\underline{Sg}_3$
T. turgidum nigro-barbatum	-	$\underline{Sg}_2$	$\underline{sg}_3$
T. dicoccum Vernal	-	$\underline{Sg}_2$	$\underline{sg}_3$
squarrosa components			
Ae. squarrosa No. 2	$\underline{sg}_1$	-	-
Ae. squarrosa Sears'	$\underline{Sg}_1^c$	-	-

better fitness to the northern region of Japan. If this is also true for wheat, it must have been very important that common wheat acquire, among other characters, strong winter growth habit by sg_1 on chromosome XVIII, in order to extend its growing area further north in the Northern hemisphere. This assumption is supported by the result of Heyne and Livers (1953) who found that F_1 mono-XVIII from the cross, Chinese Spring monosomics x Pawnee (winter variety), was resistant to winter injury, while all the other F_1 monosomics as well as disomics were sensitive.

The most effective winter habit gene, sg_1, was found by the present comparative gene analysis in a winter habit strain of Ae. squarrosa. It is, therefore, reasonable to assume that common wheat received the gene sg_1 at the time of its birth from Ae. squarrosa as one of the parents, acquiring higher adaptability to the northern climate than emmer wheat, the other parent. In other words, one of the major contributions to common wheat of the D genome donated by Ae. squarrosa seems to be the strong winter growth habit, owing to which common wheat can grow more successfully in high latitudes than emmer wheat. The high productivity of common wheat in comparison with that of emmer wheat in fall-sowing regions, especially in the northern part (in the Northern hemisphere) seems to support this viewpoint.

Accepting the hypothesis that sg_1 was transferred to common wheat at the time of its birth, the geographical distribution of sg_1 gene in Ae. squarrosa will provide another clue to the elucidation of the birthplace of common wheat. Tanaka and Yamashita (1957) and Kihara and Tanaka (1958) investigated the growth habit of Ae. squarrosa strains which they collected in Pakistan, Afghanistan and Iran. Their result is shown in Fig. 5.

There were two regions where winter habit strains of Ae. squarrosa were found; a great majority was found in northern Iran. This region, again, seems to be the most probable place for the origin of common wheat.

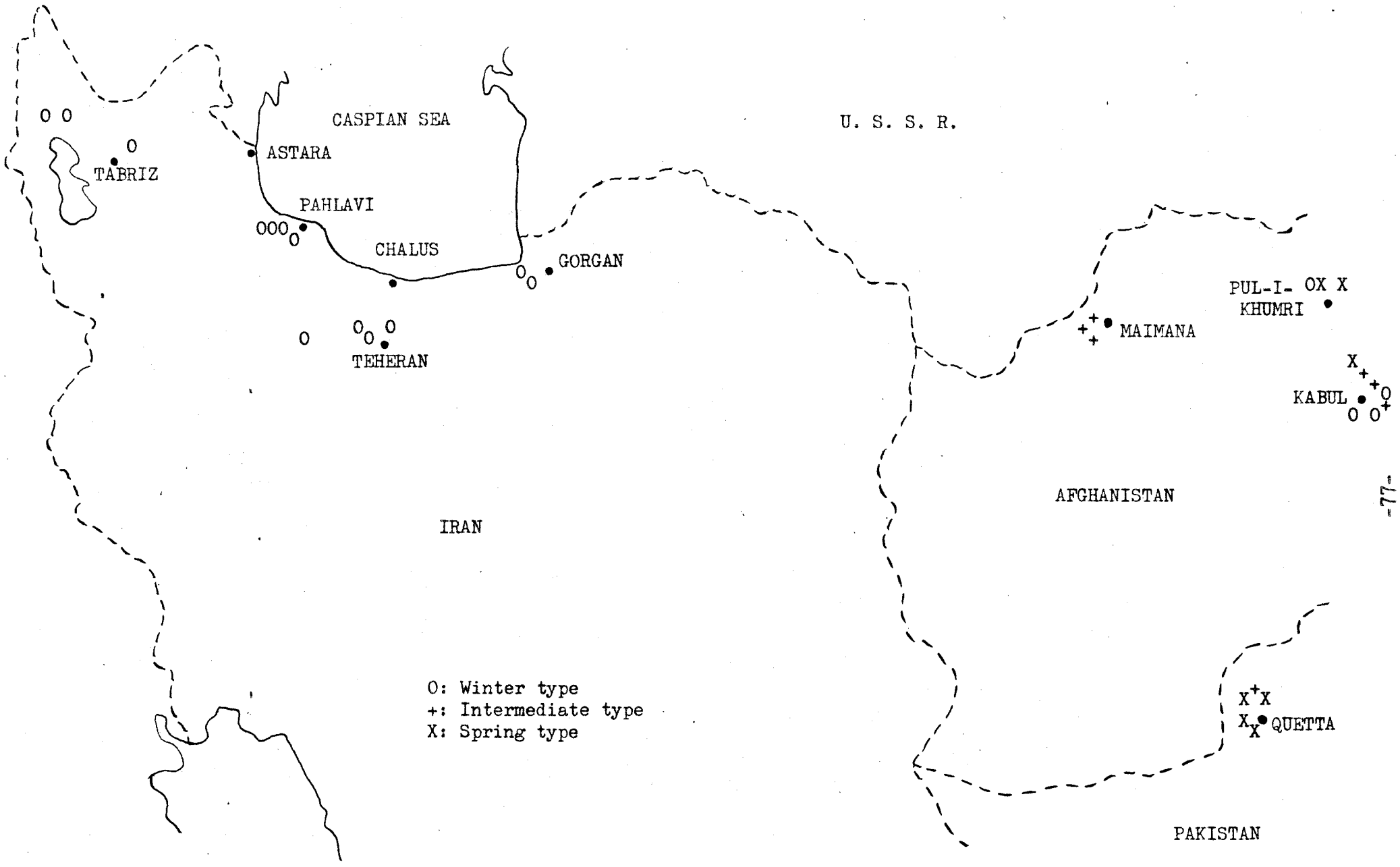


Fig. 5. Distribution of winter and spring habit strains of Ae. squarrosa.

Epstasis of the Sg_2 genes to Sg_1 genes

Chromosome XVIII of ABD-XII and -XIII should carry the sg_1 and Sg_1^c genes, respectively, because the Ae. squarrosa strain used for synthesis of ABD-XII is Kihara's No. 2 and that used for ABD-XIII is Sears'. However, F_1 mono-XVIII's of those synthetics did not show any delay of heading. F_1 data for ABD-XIII indicate that its chromosome IX derived from Vernal carries the typical spring habit allele, Sg_2. This allele is probably epistatic to Sg_1^c on chromosome XVIII of this synthetic, causing no delayed heading of F_1 mono-XVIII. Epistasis of the Sg_2 allele to the Sg_1 alleles is also suspected in ABD-XII for the following reasons, although direct proof for presence of Sg_2 in this synthetic is lacking. First of all, ABD-XII showed almost the same heading date as that of ABD-XIII, in spite of the fact that a winter habit allele, sg_1 must be present in ABD-XII but not in ABD-XIII. Secondly, T. turgidum, the emmer component of this synthetic, is a rather early spring type, suggesting the presence of a typical spring habit allele. And, thirdly, the F_1 mono-XVIII of this synthetic did not show any delay of heading, despite the hemizygous condition of the sg_1 allele.

No epistasis of Sg_2 over Sg_1 alleles is found in common wheat. As shown in the first part of this chapter, Red Egyptian, a spring variety of common wheat, carries the Sg_1^c and Sg_2 alleles, and in its crosses with Chinese Spring monosomics as the female parent, F_1 mono-XVIII showed a significant delay in heading, whose extent was very much like that obtained for the F_1 mono-XVIII of ABD-VI in this experiment. In the same manner, no epistasis of Sg_2^c over sg_1 was revealed from the cross between Chinese Spring monosomics and three winter varieties of common wheat. These facts suggest that a functional differentiation exists between the Sg_2 alleles in present-day emmer wheats and common wheat varieties.

Raw amphidiploids usually contain a large number of duplicated loci.

Some of them still remain in the present-day amphidiploids (Clausen and Cameron 1944, Sears 1954). Since their origination, however, genetic diploidization has gradually proceeded by mutations in some duplicated loci (Tsunewaki 1961a). Through this process, a complex gene might have lost a part of its function, that is now compensated by a homoeologous gene present in other genomes of the amphidiploids.

Based on such genetic diploidization, the loss of epistasis of $\underline{Sg}_2$ over $\underline{Sg}_1$ alleles during the course of evolution of common wheat can be interpreted as follows: $\underline{Sg}_2$ locus of emmer wheat is functionally the same as $\underline{Sg}_1$ locus of Ae. squarrosa. Since the spring habit allele is dominant over the winter habit allele, $\underline{Sg}_2$ or $\underline{Sg}_2^c$ of emmer wheat will express itself in synthesized 6x wheats, being epistatic over $\underline{Sg}_1^c$ or $\underline{sg}_1$ allele of Ae. squarrosa. On the contrary, $\underline{Sg}_2$ locus in common wheat has undergone some functional changes by mutations, being no longer able to mask the function of the $\underline{Sg}_1$ alleles. Similar cases were already reported by Stephens for Cl and R loci of cotton (Stephens 1951). If this would be the real mechanism, the apparent loss of epistasis of $\underline{Sg}_2$ over $\underline{Sg}_1$ alleles in common wheat is a good indication of genetic diploidization that is taking place in common wheat.

D. Conclusion

Comparative gene analysis of common wheat, emmer wheat and Ae. squarrosa, using some strains of synthesized 6x wheat, revealed that growth habit of common wheat is mainly controlled by genes belonging to three loci, $\underline{Sg}_1$, $\underline{Sg}_2$ and $\underline{Sg}_3$, and that their homologous loci are also present in its ancestors. Genotypes of their varieties or strains so far tested are collectively shown in Table 27.

$\underline{Sg}_1$, $\underline{Sg}_2$ and $\underline{Sg}_3$ are the typical spring habit alleles, $\underline{Sg}_1^c$, $\underline{Sg}_2^c$ and $\underline{sg}_3$ the semi-spring habit ones, and $\underline{sg}_1$ and $\underline{sg}_2$ the typical winter habit ones. The $\underline{sg}_1$ was much more (about three times) effective than the $\underline{sg}_2$

Table 27. Genotypes for growth habit of common wheats, emmer wheats and Ae. squarrosa strains which were studied in the present experiment.

Strains	Loci			Growth habit
	Sg_1 (XVIII)	Sg_2 (IX)	Sg_3 (XIII)	
Common wheat varieties				
T. aestivum Kharkov	sg_1	sg_2	Sg_3	winter
" Jones Fife	sg_1	sg_2	Sg_3	"
" Chinese Spring	Sg_1^c	Sg_2^c	Sg_3	spring
" S-615	Sg_1	Sg_2^c	Sg_3	"
" Prelude	Sg_1	Sg_2	sg_3	"
" Red Bobs	Sg_1	Sg_2	sg_3	"
T. compactum Elgin	sg_1	sg_2	Sg_3	winter
" Red Egyptian	Sg_1^c	Sg_2	Sg_3	spring
Emmer wheat varieties				
T. dicoccoides spontaneo-nigrum	-	sg_2	Sg_3	winter
T. dicoccum Vernal	-	Sg_2	sg_3	spring
T. durum Golden Ball	-	Sg_2^c	Sg_3	"
T. turgidum nigro-barbatum	-	Sg_2	sg_3	"
Ae. squarrosa strains				
Ae. squarrosa typica No. 2	sg_1	-	-	winter
" typica Sears'	Sg_1^c	-	-	spring

for inducing winter growth habit. Most of those alleles identified in common wheat are also present in its ancestral species.

Common wheat seems to have acquired the strong winter habit by receiving the most powerful winter habit gene, $\underline{sg_1}$, from a winter habit strain of Ae. squarrosa. This has resulted in the better adaptability of common wheat to high latitudes than that of emmer wheat. Geographical distribution of the $\underline{sg_1}$ allele in Ae. squarrosa suggested, in agreement with the result of comparative gene analysis on waxiness, that the most probable birthplace of common wheat is in the northern Iran.

In synthesized 6x wheats, epistasis of the $\underline{Sg_2}$ alleles to $\underline{Sg_1}$'s was observed in two cases, namely, the $\underline{Sg_2}$ gene to $\underline{sg_1}$ and the $\underline{Sg_2}$ to $\underline{Sg_1^c}$. However, the epistasis was not found in common wheat, at least, of the $\underline{Sg_2}$ to $\underline{Sg_1^c}$ and the $\underline{Sg_2^c}$ to $\underline{sg_1}$. The apparent loss of the epistasis of the $\underline{Sg_2}$ alleles to the $\underline{Sg_1}$'s is assumed to have been caused by genetic diploidization of the duplicated loci that has taken place in the course of evolution of common wheat.

VI. AWNEDNESS

A. Historical Review

Inheritance of awnedness has been also studied since the very beginning of the 20th Century. In many cases, a one or two gene difference was found between the awned and awnless varieties. The use of monosomics or nullisomics, however, has made it possible to detect genes with minor effects on awn expression. The results obtained are reliable but rather complicated in comparison with those reported previously. The present review, therefore, will be confined to the literatures dealing with nullisomic analysis, monosomic analysis or chromosome substitution method.

Sears (1944, 1953, 1954), Heyne and Livers (1953), Wiggin (1955), Sikka *et al.* (1959) and Kuspira and Unrau (1957, 1958) studied awn inheritance in nine common wheat varieties and proposed the following genotypes as shown in Table 28.

O'Mara (1948), Unrau (1950) and Knott (1959) ascribed awnlettedness of Marquis, Hymar and Gabo, respectively, to the B_1 gene. Campbell and McGinnis (1958) reported that Redman carries another dominant inhibitor on chromosome XVII in addition to B_1. Okamoto (1960) described an awn suppressor on chromosome V of Chinese Spring.

The gene symbols used by these workers were not always consistent. Furthermore, three additional genes had been left for designation, namely, an awn-promoting gene on chromosome XIII of Chinese Spring (Sears 1954), a minor suppressor on chromosome V of the same variety (Okamoto 1960) and an epistatic inhibitor on chromosome XVII of Redman (Campbell and McGinnis 1958). For these reasons the following symbols were proposed by Tsunewaki and Jenkins (1961) for the awn-conditioning genes after the rule set by Heyne and Livers (1953):

Table 28. Genotypes of common wheat varieties for awnedness, which were studied by previous workers.

Investigator	Varieties	Chromosomes										
		II	III	IV	VIII	IX	X	XII	XIII	XVI	XX	XXI
Sears	Chinese Spring	*			Hd	b_1	B_2		*	*	*	
Heyne & Livers	"	a_1			Hd	b_1	B_2	A_3		A_4	a_2	A_5
"	Pawnee	a_1			hd	b_1	b_2	a_3		a_4	a_2	a_5
Wiggin	Kentana 52	a_1			hd			a_3		a_4	a_2	
Sikka et al.	Rio Negro				hd	b_1	b_2					
"	C10854				hd	B_1	b_2					
"	N.P.790				hd	B_1	b_2^a					
Kuspira & Unrau	Chinese Spring	A_1	A_2		Hd	b_1	B_2	A_3				A_4
"	Thatcher	a_1	a_2		Hd^a or hd	b_1^a	b_2	a_3				a_4
"	Hope				hd	b_1	b_2					
"	Timstein	a_1	a_2		hd	B_1 or B_1^a	b_2	A_3				A_4

*: Gene located but symbols not ascribed.

Location (chromosome)	VIII	IX	X	XVII	II	XX	XII	XVI	XXI	III	IX	XIII	V
Allelic series	Hd	B_1	B_2	B_3**	A_1	A_2	A_3	A_4	A_5	A_6*	A_7*	A_8**	A_9**

* Renamed by Tsunewaki and Jenkins (1961) because the symbols originally proposed had been already registered for other series.

** Designated by Tsunewaki and Jenkins (1961)

These designations will be used throughout this thesis.

B. Experimental Results

1. Critical analysis of awnedness in eight varieties of common wheat

Monosomic analysis

Materials used here are the same as those described in a previous section dealing with growth habit. Seven varieties, namely, Red Bobs, Elgin, Jones Fife, Prelude, Kharkov, S-615 and Red Egyptian were crossed as the male parents to 21 monosomic lines of Chinese Spring. All the monosomic and disomic F_1's were examined for awn expression.

All F_1 plants produced sufficient seeds for an F_2 analysis with the following exceptions: 21 monosomic lines of Chinese Spring x Red Egyptian and Chinese Spring mono-II x Kharkov and Prelude. F_2 plants were classified at harvest as fully awned, half awned, awnletted and awnless. In F_2 populations of all crosses except the one between Chinese Spring and Red Bobs, the first two and the latter two classes were combined for statistical analysis. In the F_2 crosses between Chinese Spring monosomics and Red bobs only awnletted and awnless types were recovered and the data on these were subjected to a statistical analysis.

F_1 generation: No distinct differences in awnedness occurred between disomic and monosomic F_1 plants in any of the F_1 lines in crosses between the Chinese Spring monosomics and the varieties Red Bobs, Elgin and Jones Fife.

In crosses between the Chinese Spring monosomics and the awned varieties, F_1 plants monosomic for chromosome VIII or X of the awned variety had much longer awns than the disomic F_1 plants indicating the occurrence of complementary dominant awn-inhibiting genes on these two chromosomes of Chinese Spring. Mono-X plants were similar to the awned parent in appearance whereas mono-VIII plants had long awns only on the apical portion of the spike. This indicates that the awn inhibitor on chromosome X has a greater effect than the one on chromosome VIII.

F_2 generation: Data on F_2 segregation are summarized in Table 29 for Red Bobs, Elgin and Jones Fife and in Table 30 for Prelude, Kharkov and S-615.

Red Bobs: The disomic ratio of awnletted to awnless plants closely approached a 15:49 ratio indicating that Red Bobs and Chinese Spring differ by three genes. Because no awned plants were recovered these two varieties must have an inhibitor in common. All F_2 lines except those from F_1 plants monosomic for chromosomes II and VIII of Red Bobs segregated like the disomic F_2 lines. All plants in the F_2 lines derived from mono-II F_1 plants were completely awnless indicating that an epistatic awn inhibitor exists on chromosome II of Red Bobs. Mono-VIII F_2 populations produced a high frequency of awnletted plants suggesting that chromosome VIII of Red Bobs carries the recessive allele of the awn-inhibitor located on chromosome VIII of Chinese Spring. The third inhibitor that differentiates these two varieties was not located from monosomic analysis. The common inhibitor must be located on chromosome X of Red Bobs, because Chinese Spring is known to carry an inhibitor on this chromosome and mono-X F_2 populations segregated in the same manner as the disomic F_2s.

Elgin and Jones Fife: The F_2 disomic populations, in crosses between Chinese Spring and each of the varieties Elgin and Jones Fife, segregated in a 15:1 ratio of awnletted or awnless to awned or half-awned. F_2

Table 29. F_2 segregation of awn types in the crosses between Chinese Spring monosomics and Red Bobs, Elgin or Jones Fife.

F_2 lines	F_2s between Chinese Spring monosomics and									
	Red Bobs			Elgin		Jones Fife		Elgin and Jones Fife		
	No. of plants		x^2 (15:49)	No. of plants		No. of plants		No. of plants		x^2 (1:15)
	±	-		+	-	+	-	+	-	
Disomic	208	705	.22	36	691	50	721	86	1,412	.66
Mono- I	20	47	1.53	10	94	5	23	15	117	5.89
" II	0	70	21.43**	7	85	7	70	14	155	1.20
" III	34	132	.81	4	65	3	19	7	84	.32
" IV	28	109	.69	2	68	3	62	5	130	1.50
" V	40	128	.01	6	45	2	54	8	99	.27
" VI	29	93	.01	7	72	4	80	11	152	.07
" VII	14	27	2.62	1	36	6	70	7	106	.00
" VIII	68	115	19.20**	11	47	10	42	21	89	30.96**
" IX	20	91	1.82	0	64	0	63	0	127	8.47**
" X	23	52	2.18	20	75	19	65	39	140	73.72**
" XI	46	110	3.18	4	92	2	59	6	151	1.58
" XII	19	67	.09	4	58	2	72	6	130	.78
" XIII	12	48	.40	3	45	2	40	5	85	.07
" XIV	35	94	.98	6	78	2	63	8	141	.20
" XV	42	141	.02	2	52	6	97	8	149	.36
" XVI	24	55	2.12	7	91	3	85	10	176	.24
" XVII	24	54	2.34	10	94	9	97	19	191	2.81
" XVIII	32	105	.00	13	137	8	113	21	250	1.04
" XIX	18	59	.00	5	66	6	71	11	137	.35
" XX	10	46	.97	3	109	2	28	5	137	1.80
" XXI	18	47	.66	6	95	2	51	8	146	.29

(±) and (-) of Red Bobs indicate awnletted and awnless plants, respectively.

(+) and (-) of the other varieties indicate fully or half awned plants and awnletted or awnless plants, respectively.

**: Significant at the 1% level.

Table 30. F_2 segregation of awn types in the crosses between Chinese Spring monosomics and three awned varieties.

F_2 lines	Prelude		Kharkov		S-615		Total		x^2 (1:3)
	No. of plants		No. of plants		No. of plants		No. of plants		
	+	-	+	-	+	-	+	-	
Disomic	99	264	176	616	253	704	528	1,584	.00
Mono- I	45	128	21	62	20	47	86	237	.45
" II	-	-	-	-	15	37	15	37	.41
" III	5	12	23	74	30	51	58	137	2.34
" IV	45	137	22	64	6	19	73	220	.00
" V	33	103	7	21	-	-	40	124	.03
" VI	47	107	17	46	41	107	105	260	2.76
" VII	5	12	10	19	32	68	47	99	4.03
" VIII	47	29	32	24	96	64	175	117	189.98**
" IX	39	120	20	42	37	121	96	283	.02
" X	138	64	57	40	29	12	224	116	303.00**
" XI	5	33	13	74	31	94	49	201	3.89
" XII	29	124	16	37	30	81	75	242	.30
" XIII	17	48	25	61	16	51	58	160	.30
" XIV	15	46	11	36	39	89	65	171	.81
" XV	22	73	18	44	16	47	56	164	.02
" XVI	46	144	23	54	46	101	115	299	1.70
" XVII	47	158	27	68	39	105	113	331	.05
" XVIII	42	145	36	95	34	80	112	320	.20
" XIX	29	84	16	55	26	69	71	208	.03
" XX	19	75	9	39	25	64	53	178	.52
" XXI	36	124	12	56	32	75	80	255	.22

(+) and (-) indicate fully or half awned and awnletted or awnless plants, respectively.

** : Significant at the 1% level.

populations derived from mono-VIII and mono-X F_1 plants in both series of crosses gave a higher proportion of awned plants than expected which indicate that both Elgin and Jones Fife carry the recessive alleles of the awn inhibitors located on chromosome VIII and X in Chinese Spring. The fact that no awned plants occurred in the progeny of mono-IX F_1 plants indicated that chromosome IX of both Elgin and Jones Fife carries an awn inhibitor which must be dominant because of the similarity in appearance of the mono-IX and disomic F_1 plants. The apparent digenic ratio of 15:1 obtained in the F_2 disomic population did not agree with the results of monosomic analysis which suggested a three allele-pair difference. This discrepancy suggests that fourth allele pair is involved in segregation of awn types resulting in a tetragenic F_2 ratio of 240:16, i.e., 15:1.

Prelude, Kharkov and S-615: The F_2 populations of crosses between Chinese Spring and each of the varieties Prelude, Kharkov and S-615 segregated in a ratio of 3:1 of awnletted or awnless to awned or half-awned. Only ratios in F_2 populations derived from mono-VIII and mono-X F_1 plants in each of the three series of crosses were significantly different from the disomic 3:1 F_2 ratio. In each of these populations a higher proportion of awned plants than expected was produced. These facts agree with the F_1 data that Chinese Spring carries two dominant inhibitors and the awned varieties carry their recessive alleles on chromosomes VIII and X. The apparent monogenic ratio obtained from the F_2 disomic populations can not be explained on the basis of two pairs of alleles indicated by monosomic analysis. The discrepancy between these results indicated that a third allele pair is involved in controlling awnedness, resulting in a trigenic F_2 ratio of 48:16, i.e., 3:1.

Conventional analysis

The eight varieties, including Chinese Spring, were crossed in diallel combinations, and the F_1 phenotype and F_2 segregation were observed.

In the F_1 generation no phenotypic differences occurred between reciprocal crosses. Crosses between Red Bobs and all other varieties produced awnless F_1 plants, crosses between Chinese Spring and awnletted or awned varieties produced awnletted plants and crosses between awnletted or awnletted and awned varieties produced only awnletted F_1s. Crosses between awned varieties produced only awned plants.

The data on F_2 segregation are recorded in Table 31.

The data on F_2 of the crosses between Chinese Spring and all the other varieties have already been analyzed and discussed in the previous section.

Crosses between Red Bobs and awnletted varieties did not segregate any awned plants, indicating that they must have an epistatic inhibitor in common. This inhibitor must be the dominant one carried on chromosome IX.

Crosses between Red Bobs and awned varieties segregated not-awned and awned plants in a trigenic ratio of 55:9. This ratio would be expected because Red Bobs carries three inhibitors on chromosomes II, IX and X whereas the awned varieties carry none of these inhibitors.

The F_2 of the cross between Jones Fife and Elgin did not segregate any awned plants indicating that they carry the same inhibitor. This result confirms the findings of monosomic analysis that both varieties carry an inhibitor on chromosome IX.

The F_2 of crosses between awnletted and awned varieties segregated not-awned and awned plants in a 3:1 ratio, indicating that these two classes of varieties differ only in carrying alternate alleles of one gene. This fact confirms the findings of monosomic analysis which showed the awnletted varieties carry a dominant inhibitor on chromosome IX whereas the awned varieties do not.

The F_2 populations of crosses between awned varieties did not segregate any awnless plants; this indicated that all four awned varieties have the same genotype in regard to awnedness, as was suggested from the results of monosomic analysis.

Table 31. Actual and expected segregation of awn types in the F_2 generation of diallel crosses.

Cross combination	No. of plants		Expected ratio	x^2 values
	Awned	Not-awned		
Awnless × Awnless				
Red Bobs × Chinese Spring	208+	705++	15:49	.22
Awnless × Awnletted				
Red Bobs × Jones Fife	0	281	0:1	.00
" × Elgin	0	419	0:1	.00
Chinese Spring × Jones Fife	50	721	1:15	.07
" × Elgin	36	691	1:15	2.09
Awnless × Awned				
Red Bobs × Prelude	30	145	9:55	1.37
" × Red Egyptian	18	145	9:55	1.23
" × Kharkov	60	334	9:55	.44
" × S-615	41	221	9:55	.55
Chinese Spring × Prelude	99	264	1:3	1.00
" × Red Egyptian	105	270	1:3	1.80
" × Kharkov	176	616	1:3	3.26
" × S-615	253	704	1:3	1.05
Awnletted × Awnletted				
Jones Fife × Elgin	0	199	0:1	.00
Awnletted × Awned				
Jones Fife × Prelude	17	53	1:3	.02
" × Red Egyptian	63	202	1:3	.21
" × Kharkov	54	175	1:3	.25
" × S-615	115	313	1:3	.80
Elgin × Prelude	92	287	1:3	.11
" × Red Egyptian	63	154	1:3	1.88
" × Kharkov	64	154	1:3	2.21
" × S-615	106	334	1:3	.19
Awned × Awned				
Prelude × Red Egyptian	97	0	1:0	.00
" × Kharkov	50	0	1:0	.00
" S-615	109	0	1:0	.00
Red Egyptian × Kharkov	180	0	1:0	.00
" × S-615	162	0	1:0	.00
Kharkov × "	418	0	1:0	.00

+: Number of awnletted plants. ++: Number of awnless plants.

Summary

From the results of monosomic and conventional analyses, the following genotypes can be proposed for the eight varieties under study as shown in Table 32.

Awnlessness of Chinese Spring is attributable to two inhibitors Hd and B_2 while that of Red Bobs is controlled by the presence of inhibitors B_1 and B_2 and the absence of a promoter a_1 gene. Awnlettedness of both Elgin and Jones Fife is ascribed to the B_1 gene. A fully awned variety carries all the promoting genes but none of the inhibitors.

So far as these major genes are concerned, the monosomic and the conventional methods of analysis provided comparable results. However, a discrepancy was found between the two methods in two cross combinations, namely, Chinese Spring x awned varieties and Chinese Spring x awnletted varieties. In these crosses 3:1 and 15:1 F_2 ratio of awnletted or awnless to awned or half-awned were obtained instead of the di- and trigenic ratios expected, respectively, from the results of monosomic analysis. Sears (1954) and Heyne and Livers (1953) already showed that chromosome XVI of Chinese Spring carries an awn-inhibitor with a minor effect. Assuming that the homozygous condition of this gene prevents awn development in plants with a genotype either hd hd B_2 b_2 or Hd hd b_2 b_2, which are otherwise awned, the 3:1 and 15:1 ratios are expected in the F_2's of the crosses Chinese Spring x awned varieties and Chinese Spring x awnletted ones, respectively. Based on the same assumption, 11:5 and 59:5 ratios of not-awned to awned are expected for the F_2's of mono-XVI F_1 plants produced from the crosses of Chinese Spring mono-XVI by awned and awnletted varieties, respectively. Actual F_2 ratios do not contradict the expected ones in both cases. From those considerations, the apparent discrepancy found between the two methods of analysis may be ascribed to the inhibitor on chromosome XVI of Chinese Spring, whose effect could not be detected by monosomic analysis.

Table 32. Haploid genotypes of the eight common wheat varieties with regard to awnedness.

Varieties	Allelic series (chromosomal locations)						
	Hd (VIII)	B_1 (IX)	B_2 (X)	B_3 (XVII)	A_1 (II)	A_2 (XX)	A_8 (XVII)
Chinese Spring (awnless)	Hd	B_1	B_2	b_3	a_1	a_2	a_8
Red Bobs (")	hd	B_1	B_2	b_3	A_1	a_2	a_8
Jones Fife (awnletted)	hd	B_1	b_2	b_3	a_1	a_2	a_8
Elgin (")	hd	B_1	b_2	b_3	a_1	a_2	a_8
Prelude (fully awned)	hd	b_1	b_2	b_3	a_1	a_2	a_8
Red Egyptian (")	hd	b_1	b_2	b_3	a_1	a_2	a_8
Kharkov (")	hd	b_1	b_2	b_3	a_1	a_2	a_8
S-615 (")	hd	b_1	b_2	b_3	a_1	a_2	a_8

2. Monosomic analysis of four synthesized 6x wheats

Materials and methods used are the same as those described in a previous section dealing with monosomic analysis of growth habit of the synthesized 6x wheats.

Awnedness of the F_1 hybrids between Chinese Spring monosomics and the four synthesized 6x wheats is summarized in Table 33.

F_1 mono-VIII and -X of all the four synthetics were awned owing to the lack in these F_1 monosomics of either of the two dominant complementary inhibitors, Hd or B_2, which are already known to be located, respectively, on chromosomes VIII and X of Chinese Spring. F_1 mono-II and -XX of all the synthetics and F_1 mono-XIII of ABD-XII were less awned than the corresponding disomic F_1's. This result confirms Sears' finding that chromosomes II, XX and XIII of Chinese Spring carry awn promoters, a_1, a_2 and a_8, respectively. F_1 mono-XVI of the three synthetics so far tested had longer awns than the corresponding disomics, also confirming a result of Heyne and Livers (1953) and others that chromosome XVI of Chinese Spring carries an inhibitor, A_4. The F_1 mono-IX of ABD-I was tip-awned, probably due to the lack of a weak inhibitor locating on chromosome IX of Chinese Spring.

In the F_2 generation all plants were classified into two classes, i.e., the awned and awnless as shown in Tables 34 and 35.

Disomic F_2 lines of both ABD-I and -XII segregated awned and awnless plants in a 5:11 ratio and monosomic lines of these synthetics behaved in the same way. For this reason, F_2 data of ABD-I and -XII were combined for analysis (Table 34). Disomic F_2 lines of both ABD-VI and XIII segregated awned and awnless plants in a 1:3 ratio, and corresponding monosomic lines behaved in a similar way. Therefore F_2 data of ABD-VI and -XIII were combined, too, in Table 35.

F_2 lines of mono-VIII and -X of all the synthetics so far tested segregated many more awned plants than those of corresponding disomics. This

Table 33. Awnedness of the F_1 hybrids between Chinese Spring monosomics and four synthesized 6x wheats.

F_1 lines	Male parents			
	ABD-I	ABD-VI	ABD-XII	ABD-XIII
Disomic	±	±	±	±
Mono- I	±	±	±	±
" II	±(-)	-	±(-)	±(-)
" III	±	±	±	±
" IV	±	±	±	±
" V	±	±	±	±
" VI	±	±	±	±
" VII	±	±	±	±
" VIII	+	+	+	+
" IX	±(+)	±	?	±
" X	+	+	?	+
" XI	±	±	±	±
" XII	±	±	±	±
" XIII	±	±	±(-)	±
" XIV	±	±	±	±
" XV	±	±	±	±
" XVI	?	±(+)	±(+)	±(+)
" XVII	±	±	?	±
" XVIII	±	±	±	±
" XIX	±	±	±	±
" XX	±(-)	-	±(-)	±(-)
" XXI	±	±	±	±

-: awnless, ±(-): slightly awnletted, ±: awnletted, ±(+): tip-awned, +: awned, ?: no plants grown.

Table 34. F_2 segregation of awn types in the crosses between Chinese Spring monosomics and synthesized 6x wheats, ABD-I and XII.

F_2 lines	ABD-I		ABD-XII		Total		
	+	-	+	-	+	-	x^2 (5:11)
Disomic	97	184	237	587	334	771	.5
Mono- I	0	0	7	23	7	23	.9
" II	0	0	7	28	7	28	2.1
" III	0	1	5	25	5	26	3.3
" IV	0	1	5	8	5	9	.0
" V	0	0	11	33	11	33	.8
" VI	2	1	30	79	32	80	.4
" VII	9	13	10	20	19	33	.7
" VIII	0	0	21	21	21	21	6.9**
" IX	0	2	0	0	0	2	.0
" X	1	0	0	0	1	0	.2
" XI	3	17	18	62	21	79	4.9
" XII	0	0	7	39	7	39	5.5
" XIII	0	0	4	13	4	13	.5
" XIV	5	15	6	13	11	28	.2
" XV	0	0	11	27	11	27	.1
" XVI	0	0	29	57	29	57	.2
" XVII	0	13	0	0	0	13	4.5
" XVIII	0	0	21	51	21	51	.1
" XIX	2	2	9	31	11	33	.8
" XX	0	2	14	31	14	33	.0
" XXI	6	24	33	86	39	110	1.8

** : Significant at the 1% level.

(+) and (-) indicate awned and awnless respectively.

Table 35. F_2 segregation of awn types in the crosses between Chinese Spring monosomics and two synthesized 6x wheats, ABD-VI and -XIII.

F_2 lines	ABD-VI		ABD-XIII		Total		
	+	-	+	-	+	-	x^2 (1:3)
Disomic	249	677	81	303	330	980	.0
Mono- I	20	55	0	0	20	55	.1
" II	9	62	6	18	15	80	4.3
" III	0	5	3	3	3	8	.0
" IV	4	14	4	14	8	28	.1
" V	10	19	0	0	10	19	1.4
" VI	2	8	2	6	4	14	.0
" VII	7	20	8	17	15	37	.4
" VIII	9	6	1	1	10	7	8.6**
" IX	11	29	24	52	35	81	1.7
" X	24	6	8	4	32	10	58.7**
" XI	8	37	25	61	33	98	.0
" XII	18	52	1	13	19	65	.3
" XIII	12	45	3	2	15	47	.0
" XIV	13	28	29	62	42	90	3.3
" XV	20	57	13	36	33	93	.1
" XVI	18	31	3	9	21	40	2.9
" XVII	17	27	4	14	21	41	2.6
" XVIII	14	58	17	56	31	114	1.0
" XIX	4	14	14	26	18	40	1.1
" XX	6	15	3	9	9	24	.1
" XXI	8	14	16	47	24	61	.5

** : Significant at the 1% level.

(+) and (-) indicate awned and awnless respectively.

result confirms the F_1 data and indicates that chromosomes VIII and X of all the four synthetics carry, respectively, recessive alleles hd and b_2 of the inhibitors Hd and B_2 in Chinese Spring.

The 5:11 F_2 ratio obtained in the F_2 generation of ABD-I and -XII can be explained by two assumptions, i.e., (1) Chinese Spring and these synthetics have genotypes Hd Hd B_2 B_2 and hd hd b_2 b_2, respectively, and (2) in the F_2 generation plants having either of three genotypes Hd hd b_2 b_2, hd hd B_2 b_2 and hd hd b_2 b_2 are awned. These assumptions, of course, fit the fact that Chinese Spring (Hd Hd B_2 B_2), ABD-I and -XII (hd hd b_2 b_2), their disomic F_1's (Hd hd B_2 b_2), F_1 mono-VIII (hd - B_2 b_2) and F_1 mono-X (Hd hd b_2 -) are awnless, awned, awnletted, awned and awned, respectively.

The 1:3 F_2 ratio obtained in the F_2 generation of ABD-VI and -XIII can be explained by the same assumption as proposed for the crosses between Chinese Spring and awned common wheat varieties. In those cases, a modifier was assumed that in the homozygous condition prevents awn development in plants with a genotype either hd hd B_2 b_2 or Hd hd b_2 b_2, which would otherwise be awned. This assumption also explains the phenotypes of both parents, their disomic and monosomic F_1's and F_2 ratio as well. As both synthetics whose squarrosa component is typica No. 2 showed a 5:11 ratio while those synthesized with Sears' typica exhibited a 1:3 ratio, the modifier seems to have been derived from Sears' squarrosa strain. Its location, however, could not be determined in the present experiment.

Based on these considerations, the following genotypes can be proposed for the four 6x synthetics and their component species, as shown in Table 36.

3. Survey on the distribution of the epistatic inhibitors in various wheat species

The results described above indicate that three epistatic inhibitors, Hd, B_1 and B_2, are present in common wheat, locating on chromosome VIII (B genome), IX (A) and X (B), respectively. Therefore, their homologous

Table 36. Genotypes for awnedness of the four synthesized 6x wheats and their synthetic components.

Strains	Awnedness	Loci			
		Hd (VIII)	B_1 (IX)	B_2 (X)	A* (D)
6x synthetics					
ABD-I	awned	hd	b_1	b_2	a
ABD-VI	"	hd	b_1	b_2	A
ABD-XII	"	hd	b_1	b_2	a
ABD-XIII	"	hd	b_1	b_2	A
Emmer wheats					
T. dicoccoides spontaneo-nigrum	awned	hd	b_1	b_2	-
T. durum Golden Ball	"	hd	b_1	b_2	-
T. turgidum nigro-barbatum	"	hd	b_1	b_2	-
T. dicoccum Vernal	"	hd	b_1	b_2	-
Ae. squarrosa strains					
Ae. squarrosa typica No. 1	awnletted	-	-	-	a
Ae. squarrosa typica Sears'	"	-	-	-	A

*: Location of this locus must be in D genome but the responsible chromosome could not be identified.

genes might be found in emmer or einkorn wheat. Monosomic analysis of the four synthesized 6x wheats revealed that none of those inhibitors is present in the four emmer varieties tested. For inquiring about the origin of those genes, investigation must be carried out on a much larger scale. Fortunately, each of the three inhibitors causes remarkable inhibition of awn development, resulting in awnlessness or awnlettedness of plants, while awn promoters are present in three duplicated loci ($\underline{A}_1$, $\underline{A}_2$ and $\underline{A}_8$), no variety being known to lack more than one of the three. Therefore, a survey of awnless or awnletted varieties in the three groups of wheat should provide a useful information on the origin of those inhibitors.

The result of such survey is summarized in Table 37.

All varieties of einkorn wheat are fully awned. In emmer wheat, only four varieties are found to be awnless or awnletted, while a great majority of the examined varieties (about 96%) are fully awned. On the contrary, more than one-third of the common wheat varieties are awnless or awnletted. This information indicates that $\underline{Hd}$, $\underline{B}_1$ and $\underline{B}_2$, which are rather common in common wheat, occur very rarely in emmer wheat and are probably absent in einkorn wheat.

C. Discussion

When an increase of a gene's dosage proportionally promotes awn development it must be considered as an awn promoter whereas if the same increase proportionally depresses awn development the gene must be designated as an inhibitor. Sears' study (1954) on the dosage effect of individual chromosomes provides a critical key for classifying an awn-conditioning gene as a promoter or as an inhibitor. Chinese Spring tetrasomics of chromosomes II, XIII and XX become awned, indicating that these three homoeologous chromosomes carry awn promoters. With the exception of Red Bobs, all common wheat varieties so far tested have all three promoters.

Since the three promoters, $\underline{a}_8$ on chromosome XIII, $\underline{a}_1$ on II and $\underline{a}_2$ on

Table 37. Frequencies of the awned and awnless or awnletted varieties in various species of wheat.

Species	No. of varieties	
	awned	awnless or awnletted
Einkorn wheat		
T. aegilopoides	2	0
T. monococcum	10	0
Emmer wheat		
T. dicoccoides	8	0
T. dicoccum	17	0
T. durum	20	2
T. orientale	3	0
T. persicum	9	0
T. polonicum	7	2
T. pyramidale	10	0
T. turgidum	14	0
T. abyssinicum	2	0
Common wheat		
T. aestivum		
Japan	80	69
Pakistan, Afghanistan and Iran	156	58
Miscellaneous	13	5
T. compactum	29	17
T. macha	1	1
T. spelta	3	2
T. sphaerococcum	1	5

XX, belong to A, B and D genome, respectively, it is reasonable to assume that each of them has been derived from the respective diploid analyser of common wheat.

Chinese Spring nullisomic for chromosome VIII or X becomes awned (Sears 1954), suggesting that inhibitors are located on these chromosomes. Apparently, chromosome IX of Elgin and many other varieties carries another inhibitor. Effects on awn expression of those three inhibitors, Hd on chromosome VIII (B genome), B_1 on IX (A) and B_2 on X (B), are so remarkable that the presence of either gene can be easily investigated by morphological observation of plants. Such an investigation was undertaken with representatives of three groups of wheat, which were at the author's hand.

The result indicated that all varieties of einkorn had fully developed awns. This fact suggests that the gene B_1 is not present in this group of wheat. In emmer wheat, a great majority of varieties were fully awned. Consequently, Hd, B_1 and B_2 occur very rarely in this wheat. Four awnless or awnletted emmer varieties, which were found in this investigation, belong either to T. durum or T. polonicum, both being the most advanced cultivated forms of emmer wheat. On the contrary, frequencies of the three inhibitors are high in all species of common wheat, as revealed by monosomic analysis as well as by a morphological investigation of a large number of varieties.

Taking those facts into account, it is reasonable to assume that all three inhibitors, Hd, B_1 and B_2, were originated in common wheat, being later introduced into emmer wheat through occasional production of pentaploid hybrids with awnless or awnletted common wheat.

The frequency of inhibitors is significantly higher in Japanese local varieties than in those collected in Pakistan, Afghanistan and Iran. No critical analysis, however, has been carried out in order to estimate the frequency of the individual genes in these populations. It is one of the

future problems to investigate the frequency of each of the three genes, Hd, B_1 and B_2, in various parts of the world. Such an investigation will provide a useful information on the phylogenetic differentiation of common wheat.

D. Conclusion

Monosomic and conventional analyses of the eight varieties of common wheat revealed that awnlessness of Chinese Spring is ascribed to two inhibitors Hd and B_2, while that of Red Bobs to the presence of inhibitors B_1 and B_2 and the absence of the a_1 promoter; awnlettedness of Elgin and Jones Fife is controlled by the B_1 gene; and awnedness of Prelude, Kharkov, S-615 and Red Egyptian is due to absence of all inhibitors.

With an exception of Red Bobs, all varieties of common wheat had three awn promoters, a_1, a_2 and a_8, on chromosome II (B genome), XX (D) and XIII (A), respectively. Red Bobs lacks a_1, possessing two other promoters. Since those three chromosomes belong to the same homoeologous group, it is assumed that each of the promoters has been derived from the three different diploid ancestors of common wheat, namely, einkorn wheat, Ae. speltoides (most probably) and Ae. squarrosa.

The three epistatic inhibitors, Hd, B_1 and B_2, are located on chromosome VIII (B genome), IX (A) and X (B), respectively. They are rather common in all species of common wheat. On the contrary, they were rarely found in emmer wheat and are probably absent in einkorn wheat. From these facts it is concluded that they were originated in the hexaploid wheat, having been secondarily introduced into some emmer wheats by occasional formation of pentaploid hybrids with the 6x carrier of those genes.

VII. GLUME HAIRINESS

A. Historial Review

Inheritance of glume hairiness in common wheat has been studied by many workers, all but Howard and Howard (1915) reporting 3:1 segregation of hairy and non-hairy plants in the F_2 of crosses hairy x non-hairy. This result indicates that glume hairiness is controlled by a single dominant gene. Howard and Howard (1915), on the other hand, observed 15:1 segregation of the hairy and non-hairy plants. Sears (1954) is the first who located the gene, Hg, for glume hairiness on chromosome XIV. His result was later confirmed by Tsunewaki and Jenkins (1959), Kuspira and Unrau (1960) and Tsunewaki (1961).

In emmer wheat the same mode of inheritance was reported by Malinowski (1914) and many later workers. However, which chromosome is the carrier of this gene in emmer wheat is so far undetermined.

B. Experimental Results

1. Critical analysis of the glume hairiness in common wheat

Monosomic analysis

Jones Fife and Prelude, both with hairy glumes, were crossed as the male parent with 21 monosomic lines of Chinese Spring that has non-hairy glumes. All F_1 plants derived from the crosses between those varieties and the Chinese Spring monosomic series had hairy glumes confirming the fact that hairiness is dominant.

Segregation in the F_2 generation is summarized in Table 38.

In all F_2 populations, except that derived from F_1 plants monosomic for chromosome XIV, the segregation closely approached a 3:1 ratio of hairy to non-hairy glumed plants. The segregation in F_2 populations derived from mono-XIV F_1 plants deviated highly significantly from the 3:1 ratio in both cases. Three plants in each population possessed glabrous glumes and in

Table 38. Segregation of glume hairiness in the F_2 lines of Chinese Spring monosomics x Jones Fife or Prelude.

F_2 lines		Jones Fife			Prelude		
		No. of plants		x^2 (3:1)	No. of plants		x^2 (3:1)
		Hairy	Non-hairy		Hairy	Non-hairy	
Mono-	I	23	5	.76	125	48	.70
"	II	60	17	.35	-	-	-
"	III	17	5	.06	13	4	.00
"	IV	51	14	.42	129	53	1.65
"	V	44	12	.38	102	34	.00
"	VI	62	22	.06	118	36	.22
"	VII	59	17	.28	13	4	.00
"	VIII	40	12	.10	54	22	.63
"	IX	42	12	.22	111	48	2.28
"	X	69	15	2.29	141	61	2.91
"	XI	47	14	.14	31	7	.88
"	XII	54	20	1.16	115	38	.00
"	XIII	37	5	3.84	48	17	.05
"	XIV	62	3+	14.40**	58	3+	13.12**
"	XV	69	34	3.52	69	26	.28
"	XVI	62	26	.97	146	44	.34
"	XVII	74	32	1.52	157	48	.27
"	XVIII	90	31	.02	139	48	.04
"	XIX	60	17	.35	82	31	.36
"	XX	25	5	1.11	73	21	.35
"	XXI	44	9	1.82	122	38	.13

+: All plants were apparently nullisomic.

**: Significant at the 1% level.

all cases they appeared to be nullisomic.

These facts indicate that a single dominant gene on chromosome XIV of both Jones Fife and Prelude controls glume hairiness.

Conventional analysis

Eight varieties of common wheat, i.e., Jones Fife, Prelude, Chinese Spring, Elgin, Kharkov, Red Bobs, Red Egyptian and S-615, were crossed in diallel combinations. Among those, the first two varieties had hairy glumes, while the other six non-hairy ones.

F_1 plants derived from crosses between non-hairy parents were all non-hairy. All crosses involving one or two hairy parents produced only hairy F_1 plants indicating that hairiness is dominant.

In the F_2 generation, crosses involving only hairy or only non-hairy parents produced no segregant. All crosses between hairy and non-hairy parents produced 3:1 F_2 ratios of hairy to non-hairy segregants as shown in Table 39.

These results indicate that a single dominant gene controls the expression of glume hairiness and that the two hairy varieties possess the same gene at the same locus.

Summary

The results of monosomic analysis indicated that a single dominant gene on chromosome XIV of both Jones Fife and Prelude controls glume hairiness. The conventional analysis fully supported this result, suggesting that the varieties carry the same gene at the same locus. Sears (1954) has reported that chromosome XIV of the variety, Indian, possesses a gene, Hg, for glume hairiness. The present results confirm his finding and suggest the genotype, Hg Hg, for Jones Fife and Prelude and hg hg for the other six non-hairy varieties.

Since chromosome XIV belongs to A genome, it is expected that the

Table 39. The F_2 segregation of glume hairiness in hairy by non-hairy crosses.

Cross combinations	No. of plants		x^2 (3:1)
	Hairy	Non-hairy	
Jones Fife × Chinese Spring	590	181	.95
" × Elgin	143	56	1.05
" × Kharkov	167	62	.53
" × Red Bobs	204	77	.86
" × Red Egyptian	204	61	.55
" × S-615	327	101	.45
Prelude × Chinese Spring	275	88	.11
" × Elgin	289	91	.22
" × Kharkov	35	15	.67
" × Red Bobs	124	51	1.60
" × Red Egyptian	69	32	2.41
" × S-615	84	26	.11

homologous gene might be present in both emmer and einkorn wheat.

2. Monosomic analysis of the glume hairiness in synthesized 6x wheat

ABD-VI synthesized from T. durum Golden Ball (hairy) and Sears' Ae. squarrosa (non-hairy) has hairy glumes, the gene for which was apparently derived from the emmer parent. In order to know the mode of inheritance of this character in the synthesized hexaploid, ABD-VI was crossed as the male parent with Chinese Spring monosomic series.

In the F_1 generation all the disomic and 21 monosomic F_1's had hairy glumes, again, indicating dominance of hairiness.

Segregation of the hairiness in the F_2 generation is summarized in Table 40.

In all F_2 populations, except that derived from F_1 mono-XIV, the segregation closely approached a 3:1 ratio of hairy to non-hairy plants. The segregation in F_2's derived from F_1 mono-XIV deviated highly significantly from the 3:1 ratio. Two plants of this population, both of which appeared to be nullisomic, possessed exceptionally glabrous glumes. These results indicate that a single dominant gene located on chromosome XIV of ABD-VI controls glume hairiness. Since chromosome XIV belongs to A genome, this gene is undoubtedly derived from the emmer component, Golden Ball. In a genetic study of durum varieties, Sheybani and Jenkins (1961) found that glume hairiness of Golden Ball is controlled by a single dominant gene.

The result of the present experiment suggests that the gene controlling glume hairiness of ABD-VI and T. durum Golden Ball is the same as the Hg allele of common wheat.

3. Survey of the distribution of hairy glume gene, Hg, in various wheat species

In all cases so far reported, including that of the present author's, the gene, Hg, expresses its effect at a single dose, and no epistatic

Table 40. Segregation of glume hairiness in the F_2 generation of Chinese Spring monosomics × ABD-VI.

F_2 lines	No. of plants		x^2 (3:1)
	Hairy	Non-hairy	
Disomic	703	229	.1
Mono- I	55	18	.0
" II	53	18	.0
" III	5	0	.6
" IV	12	6	.3
" V	19	10	1.4
" VI	9	1	.5
" VII	21	6	.1
" VIII	9	6	1.1
" IX	21	11	1.5
" X	22	7	.0
" XI	31	16	2.1
" XII	59	11	3.2
" XIII	40	17	.7
" XIV	37	2+	8.2**
" XV	58	20	.0
" XVI	36	13	.1
" XVII	32	12	.1
" XVIII	54	18	.0
" XIX	13	4	.0
" XX	12	11	6.4
" XXI	14	7	.8

**: Significant at the 1% level.

+: Both plants appeared to be nullisomic.

inhibitor is yet known. Based on these facts, an investigation of glume hairiness in various wheat species has been undertaken in order to clarify the distribution and the origin of Hg gene. The result is summarized in Table 41.

This result clearly indicates that both Hg and hg are present in all three groups of wheat. However, there are some remarkable differences on the distribution pattern of Hg.

In common wheat, the Japanese population (183 local varieties were examined) does not contain any variety with hairy glumes, while in other populations Hg gene is rather common (its frequency is about 32%).

In emmer wheat, both wild and cultivated species contain Hg and hg, each occurring at an appreciable frequency (44 and 56%, respectively). In einkorn wheat, on the other hand, wild T. aegilopoides possesses the gene Hg while the cultivated species, T. monococcum, contains only hg gene.

C. Discussion and Conclusion

Monosomic and conventional analyses of eight common wheat varieties indicated that glume hairiness is controlled by a single dominant gene, Hg, located on chromosome XIV belonging to A genome. Genotypes of Jones Fife and Prelude and the other six varieties are Hg Hg and hg hg respectively. The similar analysis of ABD-VI revealed that glume hairiness of this synthetic is also controlled by a single dominant gene that is derived from T. durum Golden Gall and is located on chromosome XIV, indicating the homology to the Hg gene in common wheat.

The result of a survey of the distribution of this gene in three groups of wheat strongly suggests that the following events might have occurred in the course of evolution of wheat:

(1) In common wheat both Hg and hg are present but there is undoubtedly a significant difference between their frequencies in various parts of the world. Since no variety with hairy glumes is found in any Japanese local

Table 41. Frequencies of the varieties with hairy and non-hairy glumes in various species of wheat.

Species	No. of varieties	
	Hairy	Non-hairy
Einkorn wheat		
T. aegilopoides	2	0
T. monococcum	0	10
Emmer wheat		
T. dicoccoides	5	3
T. dicoccum	4	13
T. durum	7	15
T. orientale	3	0
T. persicum	3	6
T. polonicum	6	3
T. pyramidale	3	7
T. turgidum	9	5
T. abyssinicum	1	1
Common wheat		
T. aestivum		
Japan	0	149
Pakistan, Afghanistan and Iran	76	138
Miscellaneous	4	14
T. compactum		
Japan	0	34
Pakistan, Afghanistan and Iran	1	3
Miscellaneous	0	8
T. macha	0	2
T. spelta	2	3
T. sphaerococcum	0	6

wheat, the gene, Hg, has not been introduced to Japan until very recent years.

(2) In emmer wheat Hg and hg are common in both wild and cultivated species. Therefore, Hg and hg found in common wheat seem to have been introduced from emmer wheat when the first 6x wheat was produced or, later, through formation of pentaploid hybrids between the already existing hexaploid and emmer wheats.

(3) T. aegilopoides, the wild species of einkorn wheat, has Hg, while its cultivated species contains only hg. Considering the fact that mutation of a recessive to the dominant allele occurs much more seldom than in the reverse direction, it is assumed that the gene Hg of emmer wheat was derived from einkorn wheat when the first tetraploid wheat was produced. Since introgression of genes from einkorn to emmer wheat through the formation of triploid hybrids is very difficult, the origin of hg gene in emmer wheat can be hardly traced back to einkorn wheat. It is, on the other hand, more likely that hg was originated on the tetraploid level by a recessive mutation of a preexisting Hg gene.

(4) Taking all these considerations into account, it is tentatively proposed here that T. dicoccoides, the wild emmer species, was produced from a cross between T. aegilopoides and some species of Sitopsis (most likely Ae. speltoides), followed by amphidiploidization of the hybrid. In this way, Hg of wild einkorn wheat was introduced into the wild emmer wheat, in which mutation of Hg to hg took place. Both genes originated in this way were transferred to cultivated emmer wheat at or after its differentiation from the wild form, and later incorporated into common wheat.

VIII. GENERAL DISCUSSION

A. Origin of Common Wheat

From an extensive investigation of variations in common wheat, Vavilov (1926) concluded that it was originated in the mountainous districts of South-Eastern and North-Western Afghanistan near South-Western Himalaya. On the other hand, Schiemann (1951) concluded, based on new results obtained from four German expeditions to High Asia and those from excavations lately made in Germany, that the birthplace of common wheat is Transcaucasia and that Hindu Kush is only the accumulation center of its diversity.

The results obtained from the present comparative gene analysis strongly indicate that the Ae. squarrosa strain, which contributed the D genome to common wheat, must have had in its genotype Ne_3 for progressive necrosis, W_2 i_2-W for waxiness, sg_1 for growth habit and a_2 for awnedness. Phenotypically it must have had winter habit, waxy foliage and awned spikes and had it been crossed with Macha sub., their F_1 hybrids must have been necrotic.

All squarrosa strains so far tested had Ne_3 and a_2 gene, while those with W_2, i_2-W and sg_1 were rather rare. According to Kihara and Tanaka (1958), Ae. squarrosa with waxy foliage occurs only in north-western Iran, including Teheran, Pahlavi and Tabriz. All strains collected in this region were of winter habit.

Combining the results of the present investigation with those of the expeditions made by Kihara and Yamashita, it is assumed that common wheat has been originated in north-western Iran but not in Hindu Kush or Transcaucasia. Assuming that T. spelta is the progenitor of all other 6x species, the present opinion is supported by Kuckuck's recent finding (1959) of cultivated T. spelta in a mountainous region of central Iran that has never been found either in Hindu Kush or Transcaucasia.

The emmer wheat, which donated A and B genomes to common wheat must have had the genotype Ne_1 ne_2 or ne_1 ne_2 for necrosis, W_1 i_1-W for waxiness,

a_1 a_8 hd b_1 b_2 for awnedness and Hg or hg for glume hairiness. All varieties of wild emmer, T. dicoccoides, so far tested had non-waxy foliage, indicating the presence of I_1-W or absence of W_1 gene. In fact, T. dicoccoides spontaneo-nigrum was revealed to have the genotype w_1 I_1-W. This information strongly suggests that wild emmer was not the ancestor of common wheat, in support of the viewpoint of Kihara and Lilienfeld (1949). According to Nishikawa (1964b), a great majority of dicoccoides strains have the genotype Ne_1 Ne_2 for necrosis. This fact, also, is in favor of the present hypothesis.

Some forms of T. dicoccum, T. turgidum, T. persicum and T. orientale, and many varieties of T. durum have the genotype that can be assumed as that of the possible emmer parent of common wheat. All these species are, in fact, distributed in Iran. Therefore, the present results are not sufficient to point out one of those species as being the parent of common wheat.

In this regard, however, several considerations can be made. First of all, the amphidiploid between T. persicum and Ae. squarrosa has naked grains (Kihara and Lilienfeld 1949), due to the presence of Q gene in the former species. If T. spelta is the progenitor of all common wheats as proposed in the following section, T. persicum must be ruled out from the list of the possible AB-genome donors to common wheat.

T. turgidum, T. orientale and T. durum have also naked grains, indicating the presence of Q gene. However, the nakedness of their grains is not as pronounced as that in T. persicum or T. aestivum. Apparently, those species has a less effective Q allele than that of T. persicum. This allele will be tentatively designated here as Q^w. In accordance with this fact, all hexaploid wheats synthesized from those species and Ae. squarrosa have hulled grains. According to Muramatsu (1963), chromosome XVIII of common wheat carries q_3 gene with a weak effect on spelt expression. A chromosome

of Ae. squarrosa, that is homologous to chromosome XVIII of common wheat, might have a stronger spelt allele on the q_3 locus. In other words, a q_3 allele with less effect for spelt character seems to have been selected for a long time in common wheat, while Ae. squarrosa still preserves the original allele. This might be the most probable explanation why naked emmer wheats with Q^w gene give rise, without exception, to hulled hexaploids when combined with Ae. squarrosa. Under these circumstances, T. turgidum, T. orientale and T. durum can not be considered as the possible emmer parent of common wheat, even though amphidiploids between these species and Ae. squarrosa are of spelt type.

Consequently, T. dicoccum, that possesses a typical q gene, is the only species which can be assumed as the donor of AB genomes to common wheat.

B. Differentiation of Common Wheat

All strains of Ae. squarrosa and a great majority of common wheat varieties possess Ne_3 for necrosis. This fact indicates that the progenitor of common wheat received Ne_3 gene from Ae. squarrosa. T. macha differs from all other 6x species by possessing ne_3 gene. According to Kuckuck (1964a), T. macha must be included in T. spelta, because both have the spelt gene, q, that is one of the species-specific genes in common wheat. The author (unpublished) obtained a result that supports Kuckuck's proposal. These facts lead to the conclusion that T. macha has differentiated from T. spelta accompanied by the mutation of Ne_3 to ne_3.

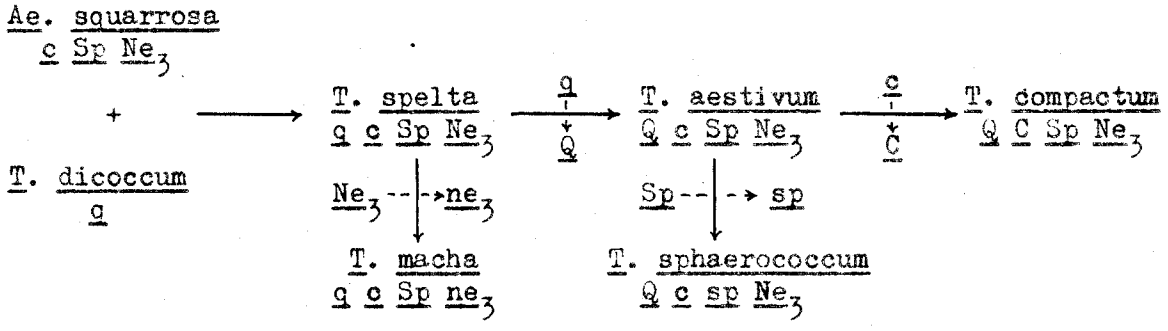
The relationship between T. spelta and T. aestivum is not conclusive. T. spelta could have been produced from a cross between Ae. squarrosa and T. dicoccum having gene q, while T. aestivum might have been originated from a cross between Ae. squarrosa and T. persicum having gene Q. In fact, both T. dicoccum and T. persicum are distributed in northern Iran. However, T. spelta, including T. macha, has more undesirable characters for cultivation

than T. aestivum. Among those brittle ear rachis and hulled grain are decisively unfavorable. Therefore, it seems that T. spelta could have had little chance to be domesticated, if T. aestivum with tough ear rachis and naked grains had been the first to appear.

Based on this consideration, it is assumed here that T. spelta is the progenitor of common wheat; the differentiation of T. aestivum from T. spelta was accompanied by the mutation of q to Q gene. This hypothesis is partly supported by Kuckuck's discovery of T. spelta in Iran, where common wheat is assumed to have been originated.

The differentiation of two other 6x species, namely, T. compactum and T. sphaerococcum, from T. aestivum was already ascribed by Sears (1956) to mutations of c to C and Sp to sp, respectively.

Based on all those informations, the phylogenetic relationships among five species of common wheat can be diagrammatically shown as follows:



Note: --→ indicates major gene mutation occurred at the time of species differentiation.

It must be, however, remembered that there might have been rather frequent exchanges of genes among different species of common wheat. For example, the relative frequencies of three pairs of necrosis genes in T. aestivum and T. compactum are rather similar, indicating frequent gene exchanges between these two species. There, also, might be some mutual gene transfers between T. spelta cultivated in Central Europe and T. aestivum and between T. sphaerococcum, an endemic species of India and T. aestivum. No gene exchange is assumed to have occurred among T. spelta, T. macha and

T. sphaerococcum, and also between T. compactum and T. macha or T. sphaerococcum, because of their geographical isolation. However, further detailed analysis with a large number of variations of T. macha, T. spelta and T. sphaerococcum is required for critical evaluation of the mutual gene exchanges among those species.

C. Origin and Differentiation of Emmer Wheat

Since the present investigation has been mainly concerned with the origin of common wheat, only little effort has been made to elucidate the origin and differentiation of emmer wheat. In this regard, a further extensive investigation is needed.

The comparative gene analysis on glume hairiness revealed that Hg gene for glume hairs is present in all strains of T. aegilopoides (wild einkorn wheat) but not in T. monococcum (cultivated form of einkorn). Since this gene is abundantly found in almost all species of emmer wheat, it is reasonably assumed that emmer wheat was originated from T. aegilopoides, not from T. monococcum. When einkorn wheat was domesticated, mutation of Hg to hg gene seems to have taken place.

Comparative gene analysis on waxiness provided a further critical information on the possible progenitor of emmer wheat. Both T. aegilopoides and T. monococcum have w gene. Therefore, it is expected that the progenitor of emmer wheat must have possessed this gene. Among the seven species examined here, only T. dicoccoides, wild emmer species had w gene. This fact leads to a conclusion that T. dicoccoides is the progenitor of all emmer species.

Sarkar and Stebbins (1956) proposed from detailed comparative morphological study that the B genome donor of emmer wheat must be Ae. speltoides. Riley, Unrau and Chapman (1958) carried out comparative karyotype and genome analyses, reaching to the same conclusion on the origin of B genome. Rees (1963) measured the DNA content per nucleus of three groups of wheat

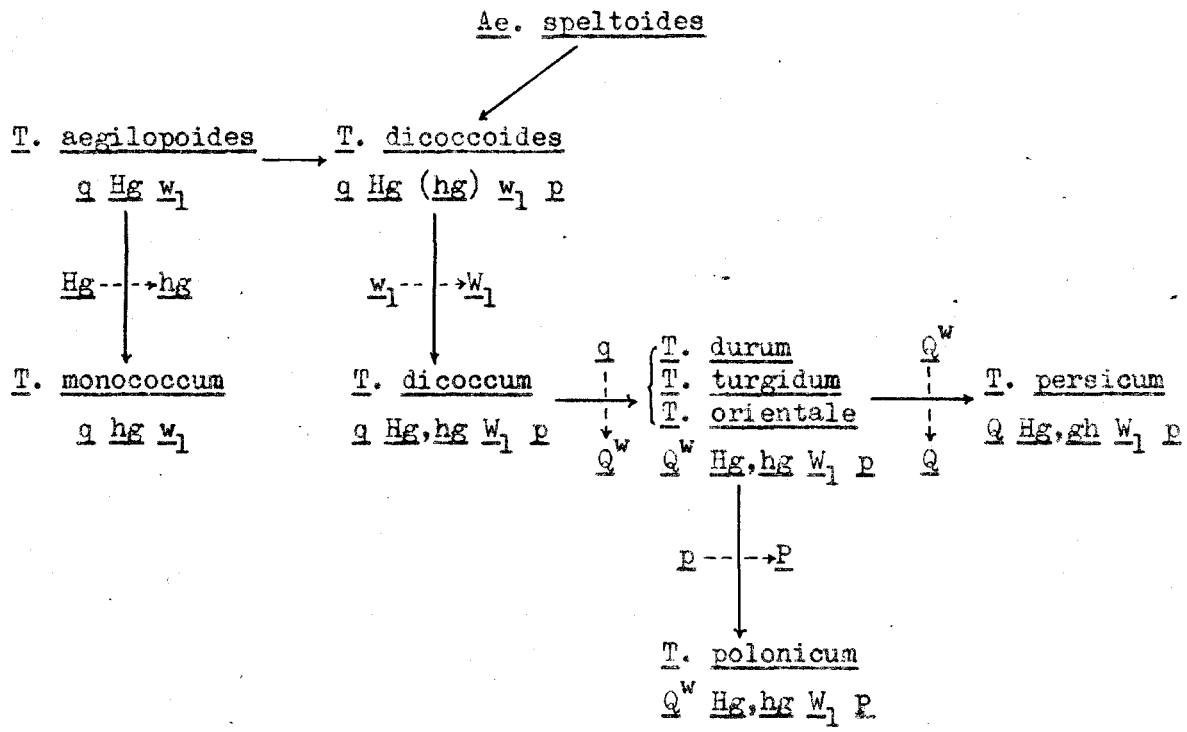
and their relatives, finding that Ae. speltoides is the most probable donor of B genome. All these informations point to the same fact that Ae. speltoides, a wild grass species, is one of the parents of emmer wheat. If the progenitor of emmer wheat was produced from Ae. speltoides and T. aegilopoides as the other parent, it must have been a wild type. The present hypothesis that T. dicoccoides is the progenitor of all emmer wheats finds a strong support in this fact.

At the synthesis of the first emmer wheat, i.e., T. dicoccoides, from Ae. speltoides and T. aegilopoides, it must have received q gene for spelt character from the einkorn parent, because this gene is located on chromosome IX in A genome and T. aegilopoides has the spelt character, as it is generally referred to as small spelt.

The first cultivated form of emmer wheat must be T. dicoccum, because it is the only species which possesses the q gene. In fact, the ear rachis of T. dicoccum is rather fragile, indicating that it is the most primitive among all cultivated emmer species.

As discussed already, T. durum, T. turgidum and T. orientale possess "Q^W" and T. persicum Q on the same locus, q. T. polonicum, that has naked grains, is different from all other emmer species by possessing P gene (Matsumura 1950), while its q allele must be Q^W, because individuals with rather tough glumes are segregated in the offspring of the cross, T. polonicum × T. aestivum.

Based on those considerations, the following phylogenetic relationships can be assumed among various species of einkorn and emmer wheats:



Note: ( ) indicates the occurrence of the recessive allele.

----→ : Major gene mutation that took place at the time of species differentiation.

IX. GENERAL CONCLUSION

Comparative gene analysis of common wheat and its direct ancestors, emmer wheat and Ae. squarrosa was carried out for five characters, namely, progressive necrosis, waxiness, growth habit, awnedness and glume hairiness. From this analysis, genic systems controlling those characters were elucidated and the number of genes involved was determined as well as the mode of their actions or interactions and their chromosomal and/or genomic locations. Conclusions of the analysis for each character was already presented in the preceding chapters. Here, only some general conclusions will be drawn.

Location of genes in common wheat: The following genes were first located and designated; For progressive necrosis, $\underline{Ne}_1$ and $\underline{ne}_1$ genes on chromosome V, $\underline{Ne}_2$ and $\underline{ne}_2$ on chromosome XIII and $\underline{Ne}_3$ and $\underline{ne}_3$ on chromosome XVI, each chromosome belonging to B, A and D genome, respectively. For waxiness, $\underline{W}_1$, $\underline{W}_1^c$ and $\underline{w}_1$ genes on chromosome XIII in A genome and $\underline{I}_2$-$\underline{W}$ and $\underline{i}_2$-$\underline{W}$ on chromosome XX in D genome. $\underline{W}_2$ and $\underline{w}_2$ are in D genome and $\underline{I}_1$-$\underline{W}$ and $\underline{i}_2$-$\underline{W}$ in A or B genome but their chromosomal locations could not be determined. For growth habit, $\underline{Sg}_1$, $\underline{Sg}_1^c$ and $\underline{sg}_1$ on chromosome XVIII in D genome, $\underline{Sg}_2$, $\underline{Sg}_2^c$ and $\underline{sg}_2$ on chromosome IX in A genome, and $\underline{Sg}_3$ and $\underline{sg}_3$ on chromosome XIII in A genome.

In addition, locations of the following genes reported by the previous workers were confirmed; For awnedness, Hd and hd on chromosome VIII in B genome, $\underline{B}_1$ and $\underline{b}_1$ on chromosome IX in A genome, $\underline{B}_2$ and $\underline{b}_2$ on chromosome X in B genome, and $\underline{A}_1$ and $\underline{a}_1$ on chromosome II in B genome. And for glume hairiness, Hg and hg on chromosome XIV in A genome.

Origin of those genes: Most of those genes were found in the ancestral species of common wheat and their chromosomal as well as genomic locations were identified through monosomic analysis of synthesized 6x wheats and/or conventional crossing experiments. However, some major genes seemed to

have originated by mutations after the formation of the hexaploid wheat. In this respect the origins of the major genes are enumerated as follows;

Genes derived from the emmer parent----$\underline{Ne_1}$, $\underline{ne_1}$, $\underline{ne_2}$, $\underline{W_1}$, $\underline{i_1}$-$\underline{W}$, $\underline{Sg_2}$, $\underline{Sg_2^c}$, $\underline{sg_2}$, $\underline{Sg_3}$, $\underline{sg_3}$, $\underline{hd}$, $\underline{b_1}$, $\underline{b_2}$, $\underline{a_1}$, $\underline{a_8}$, $\underline{Hg}$, $\underline{hg}$

Genes derived from the squarrosa parent----$\underline{Ne_3}$, $\underline{W_2}$, $\underline{i_2}$-$\underline{W}$, $\underline{sg_1}$, $\underline{a_2}$

Genes originated at the 6x level-----$\underline{Ne_2}$, $\underline{ne_3}$, $\underline{Sg_1^c}$, $\underline{Sg_1}$, $\underline{Hd}$, $\underline{B_1}$, $\underline{B_2}$, in addition to those already known, i.e., $\underline{Q}$, $\underline{C}$ and $\underline{sp}$

Loss of the epistasis: During the present investigation two cases of duplicated loci were found, those being $\underline{Sg_1}$-$\underline{Sg_2}$, for growth habit and $\underline{a_1}$-$\underline{a_2}$-$\underline{a_8}$ for awn promotion. In the former case, $\underline{Sg_2}$ alleles of emmer wheat are epistatic over $\underline{Sg_1}$ alleles of Ae. squarrosa in synthesized 6x wheats. On the other hand, the $\underline{Sg_2}$ alleles are not epistatic over the $\underline{Sg_1}$ alleles in common wheat. Such a loss of epistasis in the natural polyploid species seems to have been caused by genetic diploidization of the duplicated loci. In the case of awn promoters, allelic genes were found only in the $\underline{a_1}$ locus, so that no critical analysis could be performed.

Origin of common wheat: The results obtained strongly indicate that common wheat was first produced from an Ae. squarrosa strain having the genotype, $\underline{Ne_3}$ $\underline{W_2}$ $\underline{i_2}$-$\underline{W}$ $\underline{sg_1}$ $\underline{a_2}$ and, phenotypically, winter growth habit with waxy foliage and awned spikes crossed to an emmer wheat having genotype, $\underline{Ne_1}$ (or $\underline{ne_1}$) $\underline{ne_2}$ $\underline{W_1}$ $\underline{i_1}$-$\underline{W}$ $\underline{Sg_2}$ (or, $\underline{Sg_2^c}$ or $\underline{sg_2}$) $\underline{a_1}$ $\underline{a_8}$ $\underline{hd}$ $\underline{b_1}$ $\underline{b_2}$ $\underline{Hg}$ (or $\underline{hg}$) and, phenotypically, waxy character and fully awned spikes. Ae. squarrosa with the above-mentioned genotype was found to occur in a restricted region of north-western Iran. Based on this fact, it is concluded that in this region common wheat was originated.

Some forms of T. dicoccum, T. durum, T. orientale and T. turgidum were found to have the genotype postulated for the emmer parent of common wheat. All these species, in fact, occur in Iran. The present results, therefore, do not provide critical clues for specific determination of either of those

species as the other parent. Taking several other facts into consideration, as discussed in the previous chapter, it can be assumed that T. dicoccum is the most probable donor of AB genomes to common wheat.

Origin of emmer wheat: The present investigation did not extensively enough deal with this problem. However, the findings on glume hairiness suggest that T. aegilopoides was one of the parents of emmer wheat, and those on the waxiness indicate that T. dicoccoides might be the progenitor of all emmer species. Taking the results of some previous workers into consideration, it is concluded that the first emmer species, T. dicoccoides, was produced from T. aegilopoides and Ae. speltoides, and all other cultivated species of emmer wheat were later differentiated from T. dicoccoides.

Phylogenetic relationship among various wheat species: Based on the results obtained from the present investigation and those of the previous workers, the following phylogenetic relationship is proposed for various species of wheat, as shown in Fig. 6. Its details are discussed in the previous chapter.

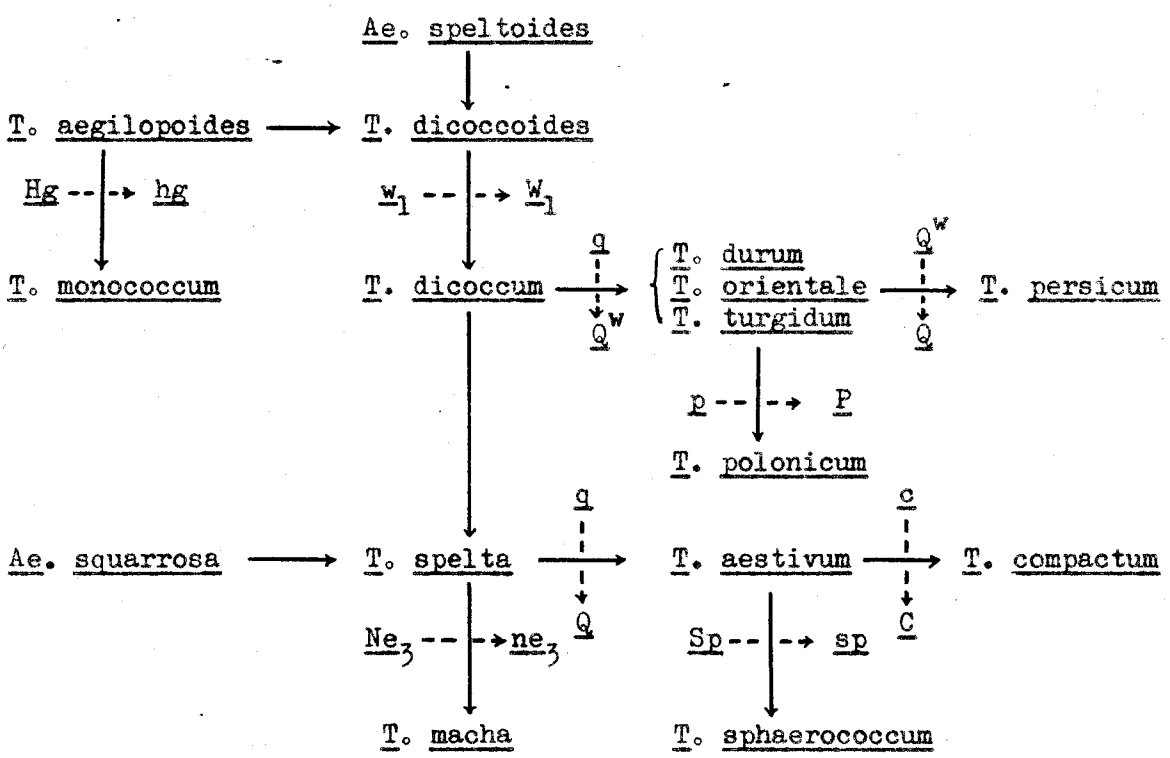


Fig. 6. Probable phylogenetic relationship among various species of wheat based on the result of comparative gene analysis.

——→ : direction of species differentiation.

- - - - → : major gene mutation that occurred at the time of species differentiation.

X. SUMMARY

1. For the study of origin and differentiation of cultivated plants, the new method of "Comparative gene analysis" has been applied to common wheat and its relatives.

According to this method, gene analysis is carried out in a given cultivated species and in parallel in its relatives under the same genetic background. Due to the results obtained, the origin of genes which are found in the cultivated species can be traced, and its coming into existence can be based on the origin of those genes.

2. Adopting this working plan, a comparative gene analysis of common wheat and its direct ancestors, emmer wheat and Ae. squarrosa, and, incidentally einkorn wheat, has been carried out for five characters, namely, progressive necrosis, waxiness, growth habit, awnedness and glume hairiness. The analysis consisted of three steps, i.e., (1) monosomic and conventional gene analyses of common wheat in order to clarify the genic system controlling each character, (2) monosomic analysis of various synthesized 6x wheats, from which the genotypes of their components, i.e., emmer wheat and Ae. squarrosa were determined in comparison with those of common wheat, and (3) survey of the distribution of those genes in a large number of varieties of common wheat and its relatives by ordinary crossing experiments or by simply observing their phenotypes.

3. Progressive necrosis in common wheat has been found to be controlled by three complementary genes, Ne_1 on chromosome V (B genome), Ne_2 on XIII (A) and Ne_3 on XVI (D). Three test varieties for those necrosis genes have been established, those being Kharkov (ne_1 Ne_2 Ne_3), Prelude (Ne_1 ne_2 Ne_3) and Macha sub. (Ne_1 Ne_2 ne_3).

The distribution of the three necrosis genes in common wheat and its ancestors has been investigated using these test varieties. A great majority of common wheat are either of $ne_1ne_2Ne_3$, $Ne_1ne_2Ne_3$ or $ne_1Ne_2Ne_3$

genotype, while of the genotypes $\underline{Ne_1}\underline{Ne_2}\underline{ne_3}$, $\underline{Ne_1}\underline{ne_2}\underline{ne_3}$ and $\underline{ne_1}\underline{ne_2}\underline{ne_3}$ each had only one representative. In emmer wheat most varieties have the genotype $\underline{Ne_1}\underline{ne_2}$, while a minor number have either $\underline{ne_1}\underline{ne_2}$ or $\underline{Ne_1}\underline{Ne_2}$. All seven strains of Ae. squarrosa have $\underline{Ne_3}$.

The genotype of emmer wheat that supplied AB genomes to common wheat is assumed to be either $\underline{Ne_1}\underline{ne_2}$ or $\underline{ne_1}\underline{ne_2}$, and that of Ae. squarrosa which supplied D genome must be $\underline{Ne_3}$. Consequently, the probable progenitor of common wheat must have been either of genotype $\underline{Ne_1}\underline{ne_2}\underline{Ne_3}$ or $\underline{ne_1}\underline{ne_2}\underline{Ne_3}$. Both $\underline{Ne_2}$ and $\underline{ne_3}$ genes of common wheat seem to have arisen at the hexaploid level.

4. Waxiness of common wheat is controlled by genes located on four loci, i.e., $\underline{W_1}$ on chromosome XIII (A genome), $\underline{W_2}$ in D genome (chromosome remains unidentified), $\underline{I_1}$-$\underline{W}$ in A or B genome and $\underline{I_2}$-$\underline{W}$ on chromosome XX (D). The $\underline{W}$ loci are for waxy genes and the $\underline{I}$-$\underline{W}$ loci for their epistatic inhibitors.

Almost all varieties of common wheat possess $\underline{W_1}$ and, probably, $\underline{W_2}$ but lack both $\underline{I_1}$-$\underline{W}$ and $\underline{I_2}$-$\underline{W}$. In emmer wheat, almost all cultivated varieties have $\underline{W_1}$ and $\underline{i_1}$-$\underline{W}$ except T. pyramidale that possesses $\underline{I_1}$-$\underline{W}$ together with $\underline{W_1}$. On the other hand, wild emmer contains $\underline{w_1}$ in addition to $\underline{I_1}$-$\underline{W}$. All varieties of einkorn wheat, including both wild and cultivated species, have $\underline{w_1}$ but not $\underline{I_1}$-$\underline{W}$. Waxy Ae. squarrosa strains have the genotype, $\underline{W_2}$ $\underline{i_2}$-$\underline{W}$, while waxless strains $\underline{W_2}$ $\underline{I_2}$-$\underline{W}$.

The presumable emmer and squarrosa parents of common wheat must have been of the genotype $\underline{W_1}$ $\underline{i_1}$-$\underline{W}$ and $\underline{W_2}$ $\underline{i_2}$-$\underline{W}$ respectively. T. dicoccoides and non-waxy squarrosa can be excluded from the list for probable parents of common wheat. The progenitor of common wheat must have been of the genotype $\underline{W_1}$ $\underline{W_2}$ $\underline{i_1}$-$\underline{W}$ $\underline{i_2}$-$\underline{W}$.

Since the occurrence of Ae. squarrosa with the genotype $\underline{W_2}$ $\underline{i_2}$-$\underline{W}$ is restricted to north-western Iran, the birthplace of common wheat is assumed to

have been in this region.

All varieties of einkorn wheat, including both T. aegilopoides and T. monococcum, have w_1 gene. Consequently, the progenitor of emmer wheat must have possessed w_1. In this respect, T. dicoccoides is the only species that is eligible for being the progenitor of emmer wheat.

5. Growth habit of common wheat is mainly controlled by genes belonging to three loci, Sg_1, Sg_2 and Sg_3, located on chromosome XVIII (D genome), IX (A) and XIII (A), respectively. Some multiple alleles are found in these loci; Sg_1, Sg_2 and Sg_3 are alleles for typical spring habit, Sg_1^c, Sg_2^c and sg_3 for semi-spring habit, and sg_1 and sg_2 for typical winter habit. The sg_1 allele is much more effective than sg_2 for the induction of winter growth habit. Most of those homologous alleles are found in the ancestors of common wheat, i.e., Sg_2, Sg_2^c, sg_2, Sg_3 and sg_3 in emmer wheat and Sg_1^c and sg_1 in Ae. squarrosa.

All waxy strains of Ae. squarrosa, which can be assumed to be the D genome donor of common wheat, have sg_1. This fact suggests that common wheat received the most powerful winter habit gene, sg_1, from its squarrosa parent, acquiring a better adaptability to high latitudes than that of emmer parent. Since the geographical distribution of the sg_1 gene in squarrosa populations is mainly concentrated in northern Iran. This too suggests that the probable birthplace of common wheat should be sought in this region.

6. Awnlessness or awnlettedness of common wheat is confirmed to be mainly controlled by three epistatic inhibitors, Hd on chromosome VIII (B genome), B_1 on IX (A) and B_2 on X (B). Awn promotion is caused by three genes, a_1 on chromosome II (B), a_2 on XX (D) and a_8 on XIII (A). All varieties except Red Bobs have the three promoters. More than 30% of common wheat varieties have one or more of epistatic inhibitors.

Almost all emmer varieties have the promoters, a_1 and a_8, and no

epistatic inhibitors. Apparently, all three inhibitors have been originated at the hexaploid level. $\underline{a}_2$ of common wheat must have been derived from its squarrosa parent.

7. Glume hairiness of common wheat is controlled by a dominant gene, Hg, located on chromosome XIV in A genome. More than 30% of common wheat varieties collected in central Asia and some other parts of the world contain Hg gene, while Japanese local varieties do not possess it. This fact indicates that the gene has not been introduced into Japan until a very recent time.

Many varieties of emmer wheat, including both wild and cultivated species, have also the Hg gene. In einkorn wheat, T. aegilopoides possesses it, while T. monococcum does not. Based on this fact it is concluded that T. aegilopoides is one of the parents of emmer wheat.

8. Based on all those results, it is concluded that common wheat was first produced from an Ae. squarrosa strain with the genotype, $\underline{Ne}_3$ $\underline{W}_2$ $\underline{i}_2$-$\underline{W}$ $\underline{sg}_1$ $\underline{a}_2$, being phenotypically of winter habit and having waxy foliage and awned spikes, and an emmer wheat with the genotype, $\underline{Ne}_1$ (or $\underline{ne}_1$) $\underline{ne}_2$ $\underline{W}_1$ $\underline{i}_1$-$\underline{W}$ $\underline{Sg}_2$ (or, $\underline{Sg}_2^c$ or $\underline{sg}_2$) $\underline{a}_1$ $\underline{a}_8$ $\underline{hd}$ $\underline{b}_1$ $\underline{b}_2$ $\underline{Hg}$ (or $\underline{hg}$), being phenotypically waxy and fully awned. From the distribution of Ae. squarrosa strains which possess the above-mentioned genotype, the birthplace of common wheat is assumed to be in the north-western part of Iran.

9. Most major genes found in the present-day common wheat are assumed to have been derived from its ancestral species. For example, $\underline{Ne}_1$, $\underline{ne}_1$ and $\underline{ne}_2$ for necrosis, $\underline{W}_1$ and $\underline{i}_2$-$\underline{W}$ for waxiness, $\underline{Sg}_2^c$, $\underline{sg}_2$, $\underline{Sg}_3$ and $\underline{sg}_3$ for growth habit, $\underline{hd}$, $\underline{b}_1$, $\underline{b}_2$, $\underline{a}_1$ and $\underline{a}_8$ for awnedness, and Hg and hg for glume hairiness seem to have been derived from emmer wheat, and $\underline{Ne}_3$ for necrosis, $\underline{W}_2$ and $\underline{i}_2$-$\underline{W}$ for waxiness, $\underline{sg}_1$ for growth habit and $\underline{a}_2$ for awnedness have been probably contributed by Ae. squarrosa.

On the other hand, some other major genes appear to have been produced

at the hexaploid level by mutations. $\underline{Ne}_2$ and $\underline{ne}_3$ for necrosis, $\underline{Sg}_1^c$ and $\underline{Sg}_1$ for growth habit and $\underline{Hd}$, $\underline{B}_1$ and $\underline{B}_2$ for awn inhibition, in addition to those already known, i.e., $\underline{Q}$, $\underline{C}$ and $\underline{sp}$, are considered to be of such origin.

10. The most probable phylogenetic relationships among various species of wheat have been outlined, as given in Fig. 6; they are based on the results obtained from the present investigation and those of the previous workers.

11. $\underline{Sg}_2$ alleles of emmer wheat are epistatic over $\underline{Sg}_1$ alleles of $\underline{Ae.}$ $\underline{squarrosa}$, when brought together in synthesized 6x wheats. On the other hand, such an epistasis of $\underline{Sg}_2$ over $\underline{Sg}_1$ alleles is not observed in common wheat. Since these two loci are considered to be the duplicated ones, the loss of epistasis in the natural polyploid seems to have been caused by genetic diploidization of the duplicated loci.

12. Kihara (1951) stated that the history of the earth is written in its layers, and the history of living organisms is inscribed in the chromosomes. A better reading of the script by means of comparative gene analysis will further elucidate the history of wheat.

XI. ACKNOWLEDGEMENT

The author wishes to express his deepest gratitude to Dr. Hitoshi Kihara, Director of the National Institute of Genetics, Japan, for his stimulating guidance and continuous encouragement throughout the course of the present investigation and for his kind permission to use his valuable materials. A part of the work was carried out in the Agronomy Department, Kansas State University, U. S. A. and in the Plant Science Division, University of Manitoba, Canada. In this regard, the author wishes to express his sincere appreciation to Dr. E. G. Heyne, Kansas State University, Dr. B. C. Jenkins and Dr. L. H. Shebeski, both of the University of Manitoba, for their kind advice and encouragement, which were given to the author during his stay in their institutions.

The present investigation was facilitated by receiving valuable materials from Dr. E. R. Sears, University of Missouri, U. S. A., Dr. B. C. Jenkins, Dr. R. C. McGinnis, both of the University of Manitoba, Canada, Dr. J. G. Th. Hermsen, University of Agriculture, Wageningen, Netherlands, Dr. M. Tanaka, Kyoto University and Mr. T. Gotô, Central Agricultural Experiment Station, Konosu. Their kind cooperation is cordially appreciated. The author is also indebted to Mr. Y. Nakai who has assisted him faithfully in this work.

The results of the investigation were summarized in the present form thanks to the warm-hearted encouragement of Dr. Ichizô Nishiyama, Professor of Kyoto University to whom the author is greatly indebted. The greatest help for the preparation of the manuscript was instructive suggestions and critical review of it by Dr. Flora A. Lilienfeld, to whom the author expresses his sincere appreciation. Thanks are also due to Miss Sumiko Ohkawa who kindly typed the whole thesis.

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