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Origin and Phylogenetic Differentiation of Common Wheat Revealed by Comparative Gene Analysis*

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INTRODUCTION

"Comparative gene analysis" is an analytical study carried out in parallel with a given crop species and its relatives in order to elucidate the origin of genes in the former. Such an analysis of several important characters gives a clear picture of the origin and differentiation of the species.

This sort of approach has already been successfully applied to barley. In common wheat, SEARS (1954) and KUCKUCK (1964) carried out gene analysis for species-specific characters, thus clarifying the origin of genes, *Q*, *C* and *sp*. NISHIKAWA (1964) and TANAKA (1965) also undertook this line of work on necrosis and dwarfness, respectively, and from their results they proposed some phylogenetic relationships among various species of wheat.

Comparative gene analysis between common wheat (genome formula AABBDD) and its two immediate ancestors, emmer wheat (AABB) and *Aegilops squarrosa* (DD), has become feasible by the completion of the monosomic series, and the production of a large number of synthesized 6x strains having different emmer and *Ae. squarrosa* strains as their synthetic components. At the same time, the collection of many varieties of wheat and its relatives by several wheat expeditions and the extensive collection of cultivated wheat varieties by several institutions have provided invaluable materials for studying the frequencies of individual genes in various taxonomically, geographically or chronologically grouped populations of common wheat and its relatives.

Comparative gene analysis has been carried out on five characters, glume hairiness, waxiness, growth habit, necrosis and chlorosis. The following four steps were taken in the present investigation:

(1) Monosomic analysis of common wheat. A limited number of common wheat varieties representing different types of variation were crossed to 21

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monosomic lines. From the results obtained in the F_1 and F_2 generations, the number of major genes controlling the character, their chromosomal as well as genomic location, and the mode of their interaction were clarified, and the genotypes of the varieties employed were determined.

(2) Monosomic analysis of synthesized 6x wheat. A certain number of synthesized 6x wheats, which were selected to cover a range of variation in their components, i.e. emmer wheat and *Ae. squarrosa*, were crossed to the same monosomic series. From the results obtained in the F_1 and F_2 generations, the genes controlling each character of the synthetics were determined and compared with those found in common wheat. Furthermore, genotypes were assigned to the strains of emmer wheat and *Ae. squarrosa* used as components of these synthetics.

(3) Survey of gene distribution. The distribution of those genes which are homologous to those identified in the above experiments, was investigated on a large scale in common wheat, emmer wheat and *Ae. squarrosa* by ordinary crossing experiments or simply by observing their phenotypes. Einkorn wheat was, in some cases, involved. From this survey, the distribution of genes in common wheat and its ancestors was clarified.

(4) Extrapolation of gene frequency. In common wheat, the frequency of each gene was compared between primitive and advanced populations in a taxonomic, chronological or geographical sense, and the genotype of the progenitor of common wheat was deduced by extrapolation of the gene frequency toward more primitiveness. By comparing the extrapolated genotype of the 6x progenitor with those of present-day emmer wheat and *Ae. squarrosa*, the origin of common wheat was discussed. Similarly, extrapolation of gene frequency between emmer and common wheat provided information on the origin of the former.

GLUME HAIRINESS

Genetic basis

A parallel variation is found in three groups of wheats. Details of the analysis of the genetic basis of glume hairiness have already been reported (Tsunewaki, 1966b). In accord with the result of previous workers, a single dominant gene, *Hg*, in chromosome 1A, was found to control glume hairiness of common wheat. A hairy-glumed 6x wheat synthesized from *T. durum* cv. Golden Ball (hairy) and *Ae. squarrosa* var. *typica* (glabrous), also carried a single dominant factor in the same chromosome. Consequently, the genes responsible for glume hairiness of emmer and common wheats appear to be homologous. According to Smith (1936) a dominant gene controls glume hairiness of einkorn wheat. Since the *Hg* genes of both emmer and common wheat belong to the A genome, it is reasonable to assume that the gene in einkorn wheat is the homologue of the *Hg* gene in polyploid wheat.

Gene distribution

Frequencies of *Hg* in various geographical populations of common and other kinds of wheat are shown in Fig. 1 and Table 1, respectively.

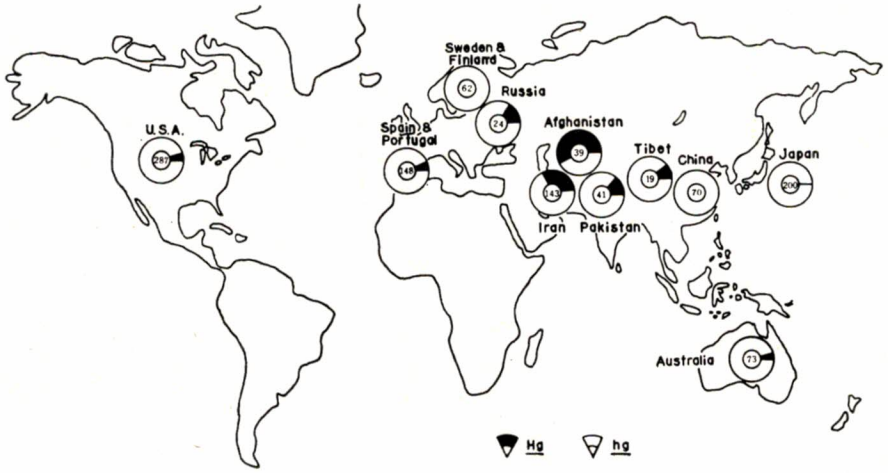

FIG. 1. Distribution of the *Hg* gene among various geographical populations of common wheat.

TABLE 1. Frequencies of varieties with hairy and glabrous glumes in various wheat species.

Species	No. of varieties			% hairy
	Total	Hairy	Glabrous	
Einkorn wheat				
T. boeoticum	5	4	1	80.0
T. monococcum	20	0	20	0.0
Emmer wheat				
T. dicoccoides	20	12	8	60.0
T. dicoccum	24	7	17	29.2
T. durum	52	18	34	34.6
T. turgidum	21	11	10	52.4
Other cult. species	33	16	17	48.5
Total of cult. species	130	52	78	40.0
Common wheat				
T. macha	13	6	7	46.2
T. spelta	96	18	78	18.8
T. aestivum	1,047	105	942	10.0
T. compactum	63	2	61	3.2
T. sphaerococcum	7	0	7	0.0
Total	1,226	131	1,095	10.7

Extrapolation of the progenitor's genotype

Frequency of *Hg* is much higher in Central Asia than in East Asia, Europe and America. Extrapolation of gene frequency from Central Asian plants and,

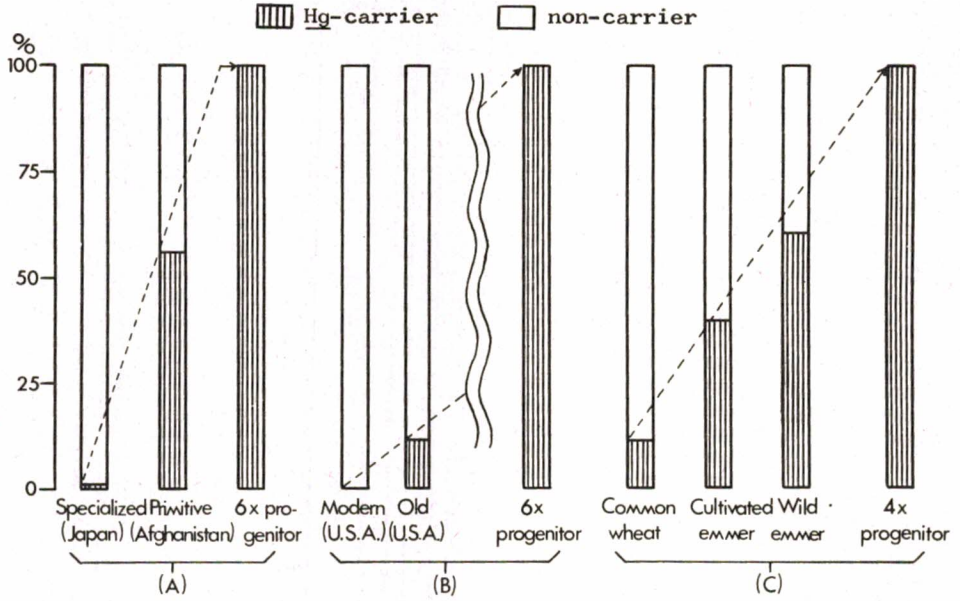

FIG. 2. Extrapolation of the glume-hair genotype for 4x and 6x progenitors. (A) and (B) represent the 6x progenitor based on geographical and chronological data, respectively. (C) represents the 4x progenitor based on taxonomical data.

for example, East Asian ones indicates, as shown in Fig. 2A, that the progenitor population of common wheat must have consisted mostly of hairy-glumed variants. The same conclusion can be drawn up by extrapolating gene frequencies of the old and modern populations of U.S.A. samples (Fig. 2B). We, therefore, may assume that the progenitor of common wheat had an *Hg* gene and, consequently, an *Hg*-carrier of emmer wheat was a parent of common wheat.

Gene frequency in the progenitor population of emmer wheat can be extrapolated in two ways; from gene frequencies of wild and cultivated emmer wheats and from those of emmer and common wheats. Both extrapolations give the same result; that the progenitor of emmer wheat had, also, an *Hg* gene. This fact tells us that the einkorn parent of emmer wheat had *Hg*. Among present-day einkorns, this gene is found only in the wild species, *T. boeoticum*. Consequently, we may conclude that wild einkorn was involved in the origin of emmer wheat. JOHNSON *et al.* (1967) reached the same conclusion from a comparison of electrophoretic patterns of seed protein.

WAXINESS

Genetic basis

Results of investigations carried out by the present author and other workers indicate that four loci are mainly concerned with the waxiness of common

wheat and its relatives. They are W_1 locus in chromosome 2B(XIII) (ALLAN and VOGEL, 1960; TSUNEWAKI, 1964), W_2 in D genome (TSUNEWAKI, 1966a), I_1-W in chromosome 2B(XIII) (DRISCOLL and JENSEN, 1964) and I_2-W in chromosome 2D (TSUNEWAKI, 1962). Dominant genes promoting waxiness are located at the former two loci, whereas epistatic inhibitors of these genes are located at the latter loci. Einkorn wheat carries neither the waxy gene nor its inhibitor. Genotypes of some representative variants are shown in TABLE 2.

TABLE 2. Genotypes on waxiness of some representatives of common wheat and its releatives.

Strains	Phenotype	Genotype				
		W_1 (2B)	W_2 (2D)	W_3 (2A)	I_1-W (2A)	I_2-W (2D)
Common wheat						
T. aestivum cultivar S-615	waxy(heavy)	W_1	W_2	w_3	i_1-W	i_2-W
T. aestivum cultivar Chinese Spring	waxy(weak)	W_1	w_2	w_3	i_1-W	i_2-W
T. aestivum Sel. 5075 (Cornell)	Waxless	W_1	?	w_3	I_1-W	i_2-W
Emmer wheat						
T. durum var. *reichenbachii*	waxy	W_1	—	w_3	i_1-W	—
T. pyramidale	waxless	W_1	—	w_3	I_1-W	—
T. dicoccoides var. *spontaneonigrum*	waxless	w_1	—	w_3	I_1-W	—
Einkorn wheat						
T. monococcum var. *vulgare*	waxless	—	—	w_3	—	—
Aegilops						
Ae. speltoides	waxy	W_1	—	—	i_1-W	—
Ae. speltoides	waxless	w_1	—	—	i_1-W	—
Ae. squarrosa	waxy	—	W_2	—	—	i_2-W
Ae. squarrosa	waxless	—	W_2	—	—	I_2-W

Gene distribution

In common wheat, almost all varieties possessed W_1 and, probably, W_2, but lacked I_1-W and I_2-W. Some 6x derivatives from pentaploid hybrids carried I_1-W from *T. dicoccoides* or *T. pyramidale*. In emmer wheat, almost all cultivated varieties had W_1 and i_1-W, while *T. pyramidale* carried I_1-W with W_1. No w_1 was found in cultivated emmer. Some wild emmer possessed w_1 in addition to I_1-W. In *Ae. squarrosa*, waxy strains had W_2 and i_2-W, while waxless ones had W_2 and I_2-W. Geographical distribution of these waxy strains is confined to northern Iran (KIHARA and TANAKA, 1958).

Extrapolation of the progenitor's genotype

Because almost all varieties of common wheat have waxy foliage, its progenitor must have been a waxy type. Consequently, its parents must have been non-carriers of *I-W* genes. The geographical distribution of waxy *Ae. squarrosa* tells us that the 6x progenitor originated in northern Iran. This conclusion, however, is acceptable only if the distribution of waxy *Ae. squarrosa* was not changed to a great extent after the origin of 6x wheat.

GROWTH HABIT

Genetic basis

In wheat and *Ae. squarrosa* three types, winter, intermediate and spring, were found. Their frequencies are summarized in TABLE 3. Comparative gene

TABLE 3. Frequency of winter, intermediate and spring types in three groups of wheat and *Ae. squarrosa**.

Species	No. strains				%
	Total	Winter	Intermediate	Spring	Spring
Common wheat					
T. aestivum	1,423	591	159	673	47
T. compactum	63	39	5	19	30
T. sphaerococcum	14	0	0	14	100
T. spelta	88	59	0	29	33
T. macha	7	7	0	0	0
Total	1,595	696	164	735	46
Emmer wheat					
T. dicoccoides	15	2	0	13	87
T. dicoccum	72	19	0	53	74
T. durum	497	42	12	443	89
T. turgidum	79	27	4	48	61
Other species	52	2	0	50	96
Total	715	92	16	607	85
Einkorn wheat					
T. boeoticum	15	12	0	3	20
T. monococcum	54	19	0	35	65
Total	69	31	0	38	55
*Ae. squarrosa***	31	17	7	7	26

* Data of 684 strains taken from "Index Seminum for *Triticum et Hordeum*" (Max-Planck Institute, Germany) and "Delectus Seminum" (Institute of Plant Industry, U.S.S.R.).
**Data taken from KIHARA *et al.* 1965.

analysis of common wheat, emmer wheat and *Ae. squarrosa* revealed that the growth habit of common wheat is mainly controlled by genes belonging to three loci, Sg_1 in chromosome 5D, Sg_2 in 5A and Sg_3 in 2B(XIII), and homologous loci for these genes are also present in emmer wheat and *Ae. squarrosa* (TSUNEWAKI, 1966a). The present results agree with the results of most previous workers, though a fourth gene in chromosome 5B and modifiers in some other chromosomes have some effect on the heading date. Genotypes of some representatives are shown in TABLE 4. Sg_1, Sg_2 and Sg_3 are alleles for spring growth habit, $Sg^c{}_1$, $Sg^c{}_2$ and sg_3 for the semi-spring habit, and sg_1 and sg_2 for the winter habit. The sg_1 was about three times more effective than sg_2 for inducing the winter growth habit. Most alleles identified in common wheat are also present in its ancestral species.

TABLE 4. Genotypes for growth habit of some strains of common wheat, emmer wheat and *Ae. squarrosa*.

Strains	Loci			Growth habit
	Sg_1 (5D)	Sg_2 (5A)	Sg_3 (2B)	
Common wheat				
T. aestivum Kharkov	sg_1	sg_2	Sg_3	winter
T. aestivum Chinese Spring	Sg^c_1	Sg^c_2	Sg_3	spring
T. aestivum Prelude	Sg_1	Sg_2	sg_3	spring
T. compactum Elgin	sg_1	sg_2	Sg_3	winter
T. compactum Red Egyptian	Sg^c_1	Sg_2	Sg_3	spring
Emmer wheat				
T. dicoccoides var. *spontaneonigrum*	—	sg_2	Sg_3	winter
T. dicoccum Vernal	—	Sg_2	sg_3	spring
T. durum Golden Ball	—	Sg^c_2	Sg_3	spring
Ae. squarrosa				
Ae. squarrosa typica No. 2	sg_1	—	—	winter
Ae. squarrosa typica Sears'	Sg^c_1	—	—	spring

Gene distribution

Geographical distribution of the three growth habit types is determined by temperature in winter. This fact explains why *T. sphaerococcum* contains only the spring type in contrast to a high frequency of winter type in other 6x species. Emmer wheat has mostly the spring type; this group having a characteristic distribution contrasting to the other wheat groups, including *Ae. squarrosa*. Distribution of three types of *Ae. squarrosa* in Central Asia was studied by KIHARA *et al.* (1965). It must be noted that all *Ae. squarrosa* strains collected in Iran were of the winter type.

Extrapolation of the progenitor's genotype

Extrapolation cannot be made in an ordinary way, because gene distribution is dependent upon natural conditions. However, the fact that 85% of emmer wheat has the spring growth habit, while only 46% of common wheat is of this type, suggests that *Ae. squarrosa,* the other parent of common wheat, was of the winter type. The author postulated from the study of waxiness that the birthplace of common wheat is in northern Iran. This postulation is strengthened

by the fact that only the winter type of *Ae. squarrosa* was found in this area. Common wheat seems to have acquired its strong winter habit by receiving the most powerful winter habit gene, sg_1, from *Ae. squarrosa*. This resulted in common wheat being more readily adaptable to high latitudes than emmer wheat.

NECROSIS AND CHLOROSIS

Genetic basis

Both necrosis and chlorosis occur in F_1 hybrids between some strains of common, emmer and synthesized hexaploid wheat. Apparently the genes respon-

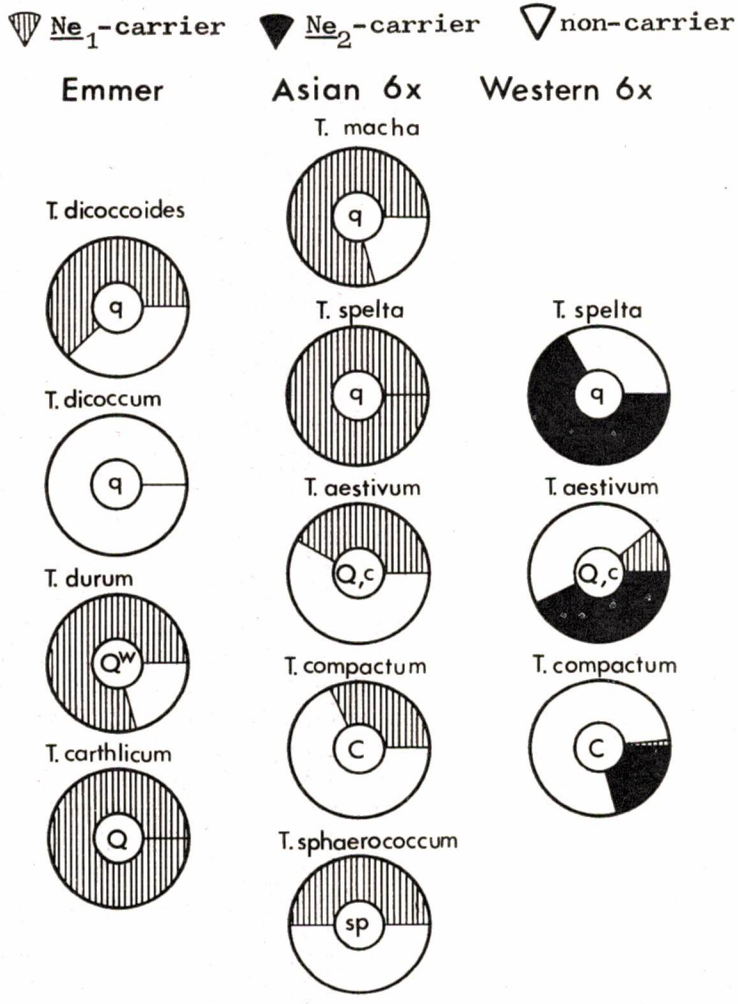

FIG. 3. Frequencies of the Ne_1- and Ne_2-carriers in various species of polyploid wheat.

sible for these traits are present alike, in common wheat, emmer wheat and *Ae. squarrosa*. Necrosis is caused by two complementary genes. One of them designated as Ne_1 was located in chromosome 5B, and the other gene, Ne_2, in chromosome 2B(XIII) (TSUNEWAKI, 1960). Chlorosis is also caused by two complementary genes, Ch_1 and Ch_2 (HERMSEN, 1966; TSUNEWAKI, 1966c). Ch_1 was located in chromosome 2A(II) (ZEVEN unpub.) and Ch_2 in 3D (TSUNEWAKI and KIHARA, 1961).

Gene distribution

Using three strains of common wheat as testers, the genotype of many varieties was determined (TSUNEWAKI, 1966c). Frequencies of three necrosis genotypes in various species of emmer and common wheats are shown in Fig. 3. In emmer wheat, Ne_1-carriers occurred frequently, while no Ne_2-carriers were found. In common wheat, Asian and Western populations were revealed to have contrasting structures; the Asian populations resembling those of the emmer population. The Western populations contained in common, Ne_2-carriers at high frequencies.

Frequencies of various chlorosis genotypes in emmer and common wheats and *Ae. squarrosa* are shown in TABLE 5. In emmer wheat, Ch_1-carriers were found in two species, *T. dicoccoides* and *T. dicoccum* though this gene was never found in other species. All *Ae. squarrosa* strains were Ch_2-carriers. A very large proportion of all common wheat species, except *T. macha*, was characterized as being Ch_2-carriers. *T. macha* was distinctly different from all others as about 80% of its varieties carried the Ch_1 instead of the Ch_2 gene.

TABLE 5. Frequencies of Ch_1- and Ch_2-carriers in emmer wheat, common wheat and *Ae. squarrosa*.

Species	No. var. tested	Ch_1-carrier		Ch_2-carrier	
		No.	%	No.	%
Emmer wheat*					
T. dicoccoides	27	8	30	—	—
T. dicoccum	13	1	8	—	—
T. durum	67	0	0	—	—
T. turgidum	6	0	0	—	—
T. carthlicum	4	0	0	—	—
Other species	12	0	0	—	—
Total	129	9	7	—	—
Ae. squarrosa	7	—	—	7	100
Common wheat					
T. spelta	104	0	0	101	97
T. vavilovi	1	0	0	1	100
T. aestivum	758	0	0	734	97
T. compactum	58	0	0	57	98
T. sphaerococcum	3	0	0	3	100
T. macha	13	11	85	0	0
Total	937	11	1	896	96

* Data for 50 varieties out of 129 taken from NISHIKAWA (1967).

Extrapolation of the progenitor's genotype

As to necrosis, two extrapolations can be made, namely, by comparisons of two taxonomical (Asian populations of hulled and naked wheats) and two geographical populations (Asian and Western naked wheats). These are shown in Fig. 4. Both comparisons indicate that the progenitor of 6x wheat was the

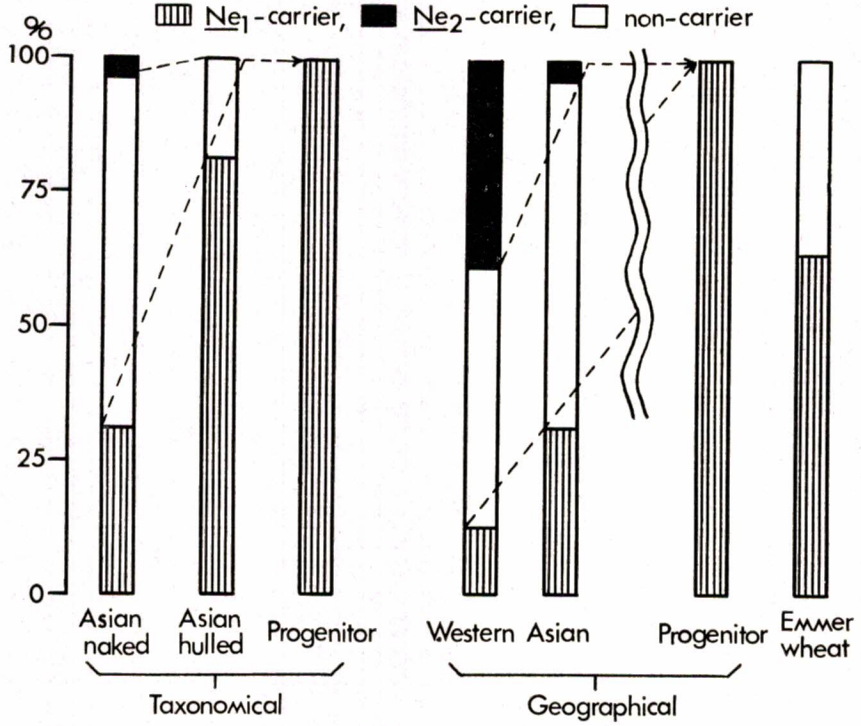

FIG. 4. Extrapolation of the necrosis genotype of the 6x progenitor.

Ne_1-carrier. This result is supported by the fact that the majority of emmer varieties carry the Ne_1 gene. The Ne_2 gene found in present-day Western common wheats seems to have lately originated at the hexaploid level.

As to chlorosis, all common wheat populations, except *T. macha,* revealed a common structure; i.e., the Ch_2-carrier occupied more than 95% of each population (TABLE 5), which indicates that the progenitor of common wheat was the Ch_2-carrier. This conclusion is further supported by the fact that all *Ae. squarrosa* strains carried the Ch_2 gene.

PHYLOGENETIC DIFFERENTIATION OF COMMON WHEAT

(1) *Origin of* T. spelta: As shown in Fig. 3. Asian and Western populations of common wheat are remarkably different from each other as to the frequencies

of the Ne_1 and Ne_2 genes. From extrapolation of the progenitor's genotype, the Asian population appears to be an original one. Parallel differentiation of all three species, *T. aestivum, T. compactum* and *T. spelta,* into two types deserves our attention. Gene exchange between *T. aestivum* and *T. compactum* seems to have been rather frequent so that their parallel differentiations are understandable. As to the differentiation of *T. spelta* into two population types, three possibilities can be considered: (i) free gene exchange between *T. spelta* and other 6x species, (ii) independent mutations of ne_2 to Ne_2 in *T. spelta* and the *T. aestivum-T. compactum* complex in Europe, and (iii) introgression to European *T. aestivum* of the spelt character from emmer wheat. The last possibility appears to be most likely, because gene exchange between *T. spelta* and other 6x species does not seem to have often taken place and independent occurrence of the same two mutations in a small area of Europe would be a rare event. Archaeological (Helbaek, 1959), linguistic (Andrews, 1964) and geobotanical evidences, also, are in favour of this possibility. We must consider the origin of the two *T. spelta* populations, Iranian and European, separately. Asian *T. spelta* is probably the progenitor of other 6x species, as proposed by Kuckuck (1959), while European *T. spelta* seems to be of a more recent origin than *T. aestivum,* as assumed by Schiemann (1951).

(2) *Origin of* T. macha: This species is distinctly different from other 6x species, having a very high frequency of the Ch_1 gene. For its origin, three possibilities are considered: (i) hybridization between a Ch_1-carrier of emmer wheat and a ch_2-carrier of *Ae. squarrosa,* (ii) two mutations ($Ch_2 \rightarrow ch_2$ and $ch_1 \rightarrow Ch_1$) in Asian *T. spelta,* and (iii) introgression to Asian *T. aestivum* of Ch_1 and *q* genes from *T. dicoccoides* or *T. dicoccum.* Because no ch_2-carrier is known in *Ae. squarrosa,* and the mutation of ch_1 to Ch_1 in a 6x ch_2-carrier, whose frequency is very low, would be very rare, the third possibility seems to be most plausible. Here, again, introgression of genes from emmer to common wheat must be assumed. The present hypothesis disagrees with the postulation of Dekaprelevich (1961), who assumed a common origin for *T. macha* and *T. spelta.*

(3) *Differentiation in* T. aestivum *and* T. compactum: Their geographical or phylogenetic differentiation as to necrosis is clearly shown in Fig. 5. Various geographical populations can be grouped into three main types, i.e., Asian (population of Central Asia, Tibet, Japan and Australia), Western (those of Central Europe and the U.S.A.) and their transitional types (those of the U.S.S.R. and Iberia). Evidently their population structure is a close reflection of their phylogenetic status.

Ecological differentiation was found in some geographical populations, such as those of Japan and the U.S.A. (Fig. 6). This fact indicates that gene exchange between winter and spring wheats is more limited than we thought.

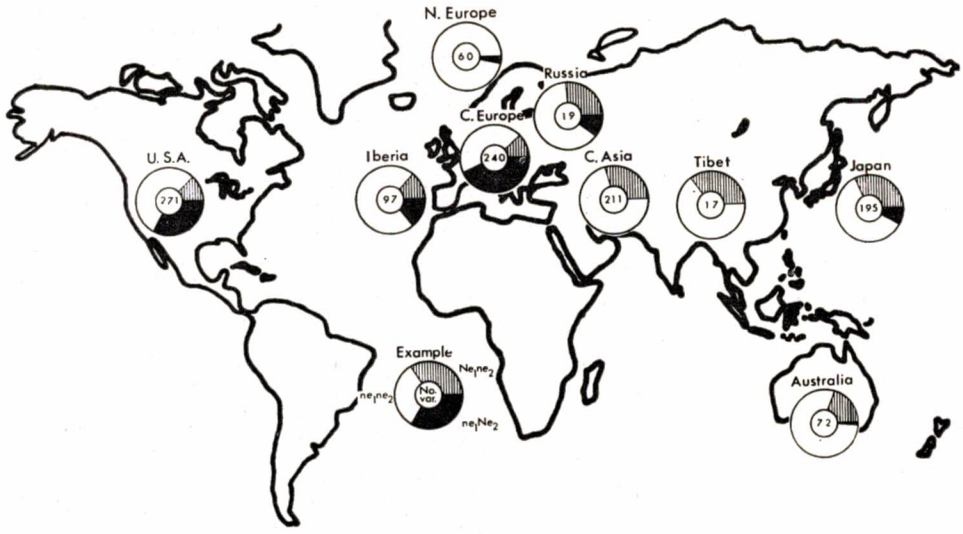

FIG. 5. Relative frequencies of three necrosis genotypes in nine geographical populations of common wheat.

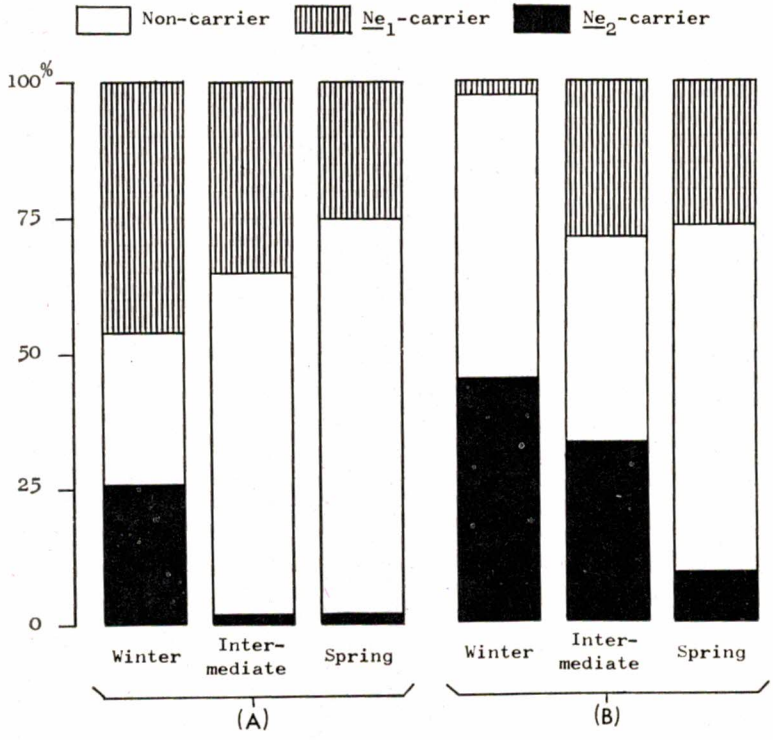

FIG. 6. Relative frequencies of the Ne_1- and Ne_2-carriers in three growth-habit types of common wheat. (A) Local population of Japan, (B) population of U.S.A.

CONCLUSION AND SUMMARY

1. "Comparative gene analysis", which consisted of four steps, namely, (i) gene analysis of common wheat, (ii) gene analysis of synthesized 6x wheats, (iii) survey of gene distribution, and (iv) extrapolation of the 6x progenitor's genotype, has been applied to five characters to clarify the origin and differentiation of common wheat. From the results obtained, the origin of genes found in common wheat was traceable, and its genesis could be based on the origin of those genes.

2. Glume hairiness of common wheat, emmer wheat and, probably, einkorn wheat is controlled by the same dominant gene, *Hg*, in chromosome 1A. Common wheat primitive populations, both geographically and chronologically, contained more *Hg*-carriers than advanced populations; thus the 6x progenitor was assumed to be an *Hg*-carrier. Overall frequency of the *Hg*-carrier was 43% in emmer wheat and 11% in common wheat. In einkorn wheat, the carrier was found only in wild species. From these facts the wild einkorn is assumed to be a parent of emmer wheat.

3. Waxiness of common wheat and its ancestors is controlled by genes at four loci, W_1 in chromosome 2B(XIII), W_2 in D genome, I_1-W in 2B(XIII), and I_2-W in 2D; the W loci for waxy genes and the I-W loci for their epistatic inhibitors. Almost all varieties of common wheat possessed W_1 and, probably, W_2 but lacked I_1-W and I_2-W. In emmer wheat, all cultivated species had W_1 and i_1-W except *T. pyramidale* which possessed I_1-W with W_1. Wild emmer contained w_1 and I_1-W. Waxy *Ae. squarrosa* strains had the genotype, $W_2\, i_2$-W, while waxless strains had $W_2\, I_2$-W.

The progenitor of common wheat must be of the genotype, $W_1\, W_2\, i_1$-$W\, i_2$-W. Consequently, its emmer and *squarrosa* parents must have had the genotype, $W_1\, i_1$-W and $W_2\, i_2$-W, respectively. Since the occurrence of *Ae. squarrosa* with the genotype, $W_2\, i_2$-W, is restricted to northern Iran, the birthplace of common wheat is assumed to be in this region.

4. The growth habit of common wheat and its ancestors is mainly controlled by genes belonging to three loci, Sg_1, Sg_2 and Sg_3, in chromosome 5D, 5A and 2B(XIII), respectively. Some multiple alleles which were found in them: Sg_1, Sg_2 and Sg_3 alleles for the spring, $Sg^c{}_1$, $Sg^c{}_2$ and sg_3 for semi-spring, and sg_1 and sg_2 for the winter habit. The sg_1 allele was much more effective than sg_2 for the induction of winter growth habit. Most of their homologous alleles were found in the ancestors of common wheat, i.e., Sg_2, $Sg^c{}_2$, sg_2, Sg_3 and sg_3 in emmer wheat, and $Sg^c{}_1$ and sg_1 in *Ae. squarrosa*. All waxy strains of the latter had sg_1, suggesting that common wheat received its most powerful winter habit gene, sg_1, from its *squarrosa* parent, acquiring a better adaptability to high latitudes than its emmer parent possessed.

5. Necrosis is controlled by two complementary genes, Ne_1 in chromosome 5B and Ne_2 in 2B(XIII). Frequencies of Ne_1 and Ne_2 genes were 20 and 25% respectively, in common wheat. In emmer wheat, Ne_1 was found in 64% of the

varieties but none of them carried Ne_2. It was assumed that the Ne_1 gene of common wheat was derived from emmer wheat, while Ne_2 originated at the 6x level. All *T. spelta, T. aestivum* and *T. compactum* showed differentiation into Asian and Western type populations. The Ne_1-carrier predominated in the former, and the Ne_2-carrier in the latter. Asian *T. spelta* was assumed to be the 6x progenitor of common wheat, while the origin of European *T. spelta* was ascribed to an introgression into European *T. aestivum* of *q* gene from *T. dicoccum*. Frequencies of two necrosis genes in various geographical populations of *T. aestivum* and *T. compactum* seem to indicate a phylogenetic relationship between populations. In some countries, ecological differentiation between winter and spring wheats was noted.

6. Chlorosis is controlled by two complementary genes, Ch_1 in chromosome 2A(II) and Ch_2 in 3D. Almost all varieties of common wheat, except those of *T. macha,* and all strains of *Ae. squarrosa* had Ch_2. This gene was evidently brought to common wheat by its *Ae. squarrosa* parent. The Ch_1 gene was found only in *T. macha, T. dicoccoides* and *T. dicoccum* and there is a severe isolation barrier between *T. macha* and other 6x species by chlorosis genes. In this regard, *T. macha* seems to have a different origin, probably from a hybridization between an Asian type *T. aestivum* and a Ch_1-carrying spelt emmer.

7. KIHARA (1951) stated, "The history of the earth is written in its layers, and the history of living organisms is inscribed in the chromosomes". Reading the scripts on wheat chromosomes by means of comparative gene analysis has provided some new evidence on the origin and differentiation of common wheat, whose main story has been already established by genome-analytical works.

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