Comparative Gene Analysis of Common Wheat and its Ancestral Species, I. Necrosis¹⁾

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There are several approaches to the study of the origin of species. Genome analysis has been successfully applied to some polyploid species such as wheat, tobacco and cotton. Chromosome analysis by means of karyotype studies, translocations or inversions has been a powerful tool for some other organisms such as *Drosophila*, maize and *Oenothera*, whose chromosome structures can be cytologically studied in detail. Comparative gene analysis of a given species and its relatives, which is the main subject of this paper, seems to provide an additional approach (cf. Nachtsheim 1959), regardless of polyploidy or ease of cytological handling.

The origin of common wheat has been nearly solved on the genome basis owing to the findings of Kihara (1924, 1944), McFadden and Sears (1944), Sarkar and Stebbins (1956) and Riley, Unrau and Chapman (1958). However, definite information is still lacking on the phylogenetic relationships among various wheat species and their relatives. In order to throw a light on those relations, the present authors have started a comparative gene analysis of common wheat and its relatives. In the present paper, the results are reported from the investigations of necrosis genes.

Since two independent reports by McMillan and Kostyuchenko in 1936 many papers have been published on complementary necrosis in common wheat. Reviewing those results as far as known to him, Hermesen (1959) proposed a "three-gene hypothesis", i.e., three dominant complementary genes, which were later designated as Ne_1 , Ne_2 and Ne_3 by Tsunewaki and Kihara (1961) and Hermesen (1961), are necessary for the expression of all types of necrosis. Tsunewaki (1960) and Tsunewaki and Kihara (1961) located Ne_1 on chromosome 5B (V), Ne_2 on 2A (XIII) and Ne_3 on 3D (XVI). Hermesen (1962) described multiple alleles, Ne_1^s , Ne_1^m , Ne_1^w and ne_1 in the Ne_1 locus, and Ne_2^s , Ne_2^{ms} , Ne_2^{wm} , Ne_2^w and ne_2 in the Ne_2 locus. Further, Tsunewaki and Kihara (1961) suspected the presence of a gene on chromosome 3B (III) that modifies the intensity of necrosis.

Nishikawa (1953, 1962), Sachs (1954) and Roy (1955) also observed similar complementary necrosis in some intergeneric hybrids between *Triticum* and *Aegilops*.

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This indicated the presence of some common necrosis genes in both these genera.

Based on their results, Tsunewaki and Kihara (1931) designated the following genotypes for three common wheat varieties;

T. aestivum Kharkov: $ne_1ne_1Ne_2Ne_2Ne_3Ne_3$

T. aestivum Prelude: $Ne_1Ne_1ne_2ne_2Ne_3Ne_3$

T. macha subletshchumicum: $Ne_1Ne_1Ne_2Ne_2ne_3ne_3$

Thus any variety producing with one of the above three varieties a necrotic F_1 must have at least a dominant allele, for which they are recessive, *i.e.* Ne_1 , Ne_2 or Ne_3 , respectively. Using these varieties as the testers, the distribution of the complementary necrosis genes in common wheat and its direct ancestors, Emmer wheat and *Aegilops squarrosa*, has been investigated.

Hermesen's three-gene hypothesis is based on a thorough survey of literature and is supported by the later results of monosomic analysis showing that the three genes are located in different chromosomes. However, no critical test of the hypothesis has been made by classical gene analysis. It was carried out in the present experiment.

Material and Methods

In order to test the validity of the three-gene hypothesis, *T. aestivum* var. Chinese Spring (haploid genotype: $ne_1ne_2Ne_3$) was reciprocally crossed to *T. macha* var. *subletshchumicum* ($Ne_1Ne_2ne_3$). The F_1 hybrids were self-pollinated or back-crossed to both parents, and segregation of the necrotic plants in the F_2 and B_1 generations was studied.

To investigate the distribution of the three necrosis genes, 20 varieties of common wheat and twelve strains of synthesized hexaploids were crossed to the three test varieties, Prelude ($Ne_1ne_2Ne_3$), Kharkov ($ne_1Ne_2Ne_3$) and *T. macha* var. *subletshchumicum* ($Ne_1Ne_2ne_3$). Their names and sources are listed in Table 1. The phenotypes of the F_1 plants produced from these crosses were observed, and the genotypes of the tested common wheat varieties and components of the synthesized hexaploids were determined.

Experimental Results

Test of the three-gene hypothesis

F_1 's between *T. macha subletshchumicum* and both Prelude and Kharkov, which were lethal due to severe necrosis, did not set any seeds, while those between the former and Chinese Spring were semi-lethal, bearing a limited number of seeds. For this reason, the three-gene hypothesis could be tested only with the hybrids of the latter cross combination.

In the course of monosomic analysis, Chinese Spring monosomics have been

crossed to *T. macha subletshchumicum*. From these crosses necrotic or normal F_1 hybrids, which were mono- or disomic, were obtained. They were self-pollinated

Table 1. List of materials

Variety or strain		Source
Common wheat		
<i>Triticum aestivum</i>	Chinese Spring	E. R. Sears
"	" Prelude	B. C. Jenkins
"	" Kharkov	"
"	" Jones Fife	"
"	" S-615	"
"	" Nowinka	J. G. Th. Hermesen
"	" Riebesel	"
"	" H ₁₁	"
"	" Marquillo	Konosu Agr. Exp. Sta.
"	" Trumbull	"
"	" American Banner	"
"	" Pawnee	"
"	" Blackhull	"
"	" Fulcaster	"
"	" <i>erythrospermum</i>	Own stock
"	<i>compactum</i> 44	"
"	<i>spelta duhamelianum</i>	"
"	<i>sphaerococcum</i>	"
"	<i>macha subletshchumicum</i>	"
"	" <i>palaeoimereticum</i>	"
Synthesized hexaploids (Emmer and <i>Aegilops</i> components)		
ABD- I	(<i>T. dicoccoides spont.</i> × <i>Ae. squarrosa typica</i> No. 2)	Kihara's ABD 1
ABD- II	(" × " <i>strang.</i> KUSE 2124)	Tanaka's ABD 9
ABD- III	(<i>T. dicoccum</i> Vernal × " <i>strang.</i> KUSE 2112)	" ABD 13
ABD- IV	(<i>T. durum</i> Gulab × " <i>strang.</i> KUSE 2118)	" ABD 14
ABD- V	(" × " <i>meyeri</i> KUSE 2144)	" ABD 16
ABD- VI	(<i>T. durum</i> Golden Ball × " <i>typica</i> Sears')	E. R. Sears
ABD-VII	(<i>T. durum</i> Pentad × " ")	"
ABD-VIII	(<i>T. orientale insigne</i> × " <i>strang.</i> KUSE 1221)	Tanaka's ABD 23
ABD- IX	(<i>T. persicum stram.</i> × " <i>typica</i> No. 2)	Kihara's ABD 4
ABD- X	(" × " <i>strang.</i> KUSE 2135)	Tanaka's ABD 11
ABD- XI	(" × " <i>meyeri</i> KUSE 2144)	" ABD 22
ABD-XII	(<i>T. turgidum nigrob.</i> × " <i>typica</i> No. 2)	Kihara's ABD 3

or backcrossed to both parents, and segregation of the necrotic plants in their progeny was studied. Results obtained are summarized in Table 2.

a_1 population represents the F_2 's from the necrotic, disomic F_1 's whose genotype is assumed according to the three-gene hypothesis to be $Ne_1ne_1Ne_2ne_2Ne_3ne_3$. a_2

Table 2. Segregation of necrotic plants in the F₂ and B₁ generations of Chinese Spring × *T. macha subletshchumicum*

Generations	Populations ¹⁾	No. of plants observed		Expected [†]			Expected ^{††}		
				No. of plants		χ^2	No. of plants		χ^2
		Necrotic	Normal	Necrotic	Normal		Necrotic	Normal	
F ₂	a ₁	72	92	69.2	94.8	0.2	74.9	89.1	0.2
"	a ₂	63	76	58.6	80.4	0.6	63.5	75.5	0.0
"	pooled	135	168	127.8	175.2	0.7	138.4	164.6	0.2
F ₂	b	1	311	0.0	312.0	(0.0)	0.0	312.0	(0.0)
B ₁	c	0	65	0.0	65.0	0.0	0.0	65.0	0.0
B ₁	d ₁	21	42	15.8	47.2	2.3	23.6	39.4	0.5
"	d ₂	17	12	7.2	21.7	17.5**	10.9	18.1	5.5*
"	d ₃	41	58	24.8	74.2	14.2**	37.1	61.9	0.7
"	d ₄	20	32	13.0	39.0	5.0*	19.5	32.5	0.0
"	pooled	99	144	60.8	182.1	32.0**	91.1	151.9	1.1

1) See text.

† Expected from segregation of the three major genes; 27:37, 0:1, 0:1 and 1:3 for a, b, c and d populations, respectively.

†† Expected from segregation of the three major genes and a modifier; 117:139, 0:1, 0:1 and 3:5 for a, b, c and d, respectively.

* Significant at the 5% level.

** Significant at the 1% level.

population represents the F₂'s from the necrotic F₁'s, which were monosomic for a non-critical chromosome and whose genotype is also supposed to be $Ne_1ne_1Ne_2ne_2Ne_3ne_3$. If the three-gene hypothesis holds true, a 27:37 ratio for necrotic *vs.* normal plants should be observed in these populations. The observed ratios proved to fit well the expectation as shown by χ^2 values in the seventh column of Table 2.

b population represents the F₂'s from normal F₁'s, which were monosomic for chromosome 3D and expected to be of the genotype, $Ne_1ne_1Ne_2ne_2ne_3-$. Based on the three-gene hypothesis, all F₂ plants in this population should be normal, and this actually occurred.

c population is the B₁ from backcrossing normal F₁ monosomics for chromosome 3D to *T. macha subletshchumicum*. This cross can be formulated as $Ne_1ne_1Ne_2ne_2ne_3- \times Ne_1Ne_1Ne_2Ne_2ne_3ne_3$. Based on the three-gene hypothesis, no segregation of necrotic plants is expected in this population, and none occurred.

d₁ population is the B₁ from backcrossing disomic, necrotic F₁'s to Chinese Spring. The genotype of the F₁ plants is expected to be $Ne_1ne_1Ne_2ne_2Ne_3ne_3$. d₂ population is the B₁ from backcrossing necrotic F₁'s monosomic for a non-critical chromosome, having the genotype $Ne_1ne_1Ne_2ne_2Ne_3ne_3$, to Chinese Spring. d₃ population is the B₁ from backcrossing normal F₁'s, which were monosomic for chromosome 3D, to Chinese Spring. The genotype of the F₁'s is assumed to be $Ne_1ne_1Ne_2ne_2ne_3-$. d₄ population is the progeny of the cross, (*T. compactum* 44 ×

T. macha subletshchumicum) $F_1 \times T. aestivum erythrospermum$. The genotype of *T. macha subletshchumicum* is $Ne_1Ne_1Ne_2Ne_2ne_3ne_3$ and that of *T. compactum* 44 and *T. aestivum erythrospermum* was found to be $ne_1ne_1ne_2ne_2Ne_3Ne_3$. If the three-gene hypothesis is correct, segregation of two pairs of genes must take place in all these populations, with a 1:3 expected ratio of necrotic *vs.* normal. However, actual segregation ratios deviated significantly from the expected ratio, as shown in the seventh column of Table 2.

The simplest modification of the three-gene hypothesis for a satisfactory explanation of all the ratios so far obtained is that the homozygous condition of a recessive gene in Chinese Spring compensates for either Ne_1 or Ne_2 . Assuming this, 117:137, 0:1, 0:1 and 3:5 ratios for the necrotic *vs.* normal plants are expected in populations a, b, c and d, respectively. The actual ratios were compared with the expected ones and proved to fit well as shown in the last column of Table 2. The modifier assumed here might be the same as the one located on chromosome 3B (III) of Chinese Spring by Tsunewaki and Kihara (1961).

Distribution of the necrosis genes in common wheat and its ancestors

Twenty varieties of common wheat and twelve strains of synthesized hexaploids were crossed to the three test varieties. Occurrence of necrosis in their F_1 's is summarized in Table 3.

Observation was made twice, namely, at the time of transplantation in fall and at shooting stage in spring. Necrosis appeared at different stages of development depending upon cross combination. This can be attributed to differences between the dominant alleles as shown by Hermesen (1962) or to a modifier as suggested by Tsunewaki and Kihara (1961).

The genotypes of the common wheat varieties and synthetic components of the artificially produced hexaploids were deduced from this experiment and are given in Table 4. In addition, *T. dicoccum* var. Khapli produced necrotic F_1 hybrids when crossed to Chinese Spring. Therefore the former must have the genotype $Ne_1Ne_1Ne_2Ne_2$. The genotypes of four additional Emmer varieties are taken from Nishikawa's results (Nishikawa 1962).

The present authors' Ne_1 and Ne_2 genes, respectively, are the same as *Le* (or *Le_1*) and *Le_2* of Caldwell and Compton (1943), Heyne *et al.* (1943) and Tsunewaki (1960), and the A and B genes of Hermesen (1957) and Schmalz (1959). From their investigations it became known that ten additional varieties of common wheat have Ne_1 , 43 varieties have Ne_2 and 44 varieties do not have either Ne_1 or Ne_2 . All these varieties so far tested have Ne_3 . From this information the relative frequencies of the three necrosis genes in common wheat and its ancestors, Emmer wheat and *Aegilops squarrosa*, are diagrammatically shown in Fig. 1.

A majority of Emmer varieties have the genotype Ne_1ne_2 , while minor fractions are either ne_1ne_2 or Ne_1Ne_2 . No variety is known to be ne_1Ne_2 . All *Ae. squarrosa*

Table 3. Phenotypes concerning necrosis of the F₁'s between three testers and common wheat and synthesized hexaploids

Tested varieties or strains	Tester (genotype)						Haploid genotype of tested vars.
	Prelude (<i>Ne₁ne₂Ne₃</i>)		Kharkov (<i>ne₁Ne₂Ne₃</i>)		<i>T. macha sublet.</i> (<i>Ne₁Ne₂ne₃</i>)		
	Early observ.*	Late observ.**	Early observ.*	Late observ.**	Early observ.*	Late observ.**	
Common wheat							
<i>T. aestivum</i> Chinese Spring	—	—	—	—	—	+	<i>ne₁ne₂Ne₃</i>
" Marquillo	—	—	—	—	—	+	"
" Trumbull	—	—	—	—	—	+	"
" American Banner	—	—	—	—	—	+	"
" Pawnee	—	—	—	—	—	+	"
" S-615	—	—	—	—	—	+	"
" <i>erythrospermum</i>	—	—	—	—	—	+	"
<i>T. compactum</i> 44	—	—	—	—	—	+	"
<i>T. spelta duhamelianum</i>	—	—	—	—	—	+	"
<i>T. macha palaeoimereticum</i>	—	—	+	+	—	—	<i>Ne₁ne₂ne₃</i>
<i>T. aestivum</i> Prelude	—	—	+	+	+	+	<i>Ne₁ne₂Ne₃</i>
" Nowinka	—	—	+	+	—	+	"
<i>T. sphaerococcum</i>	—	—	—	+	—	+	"
<i>T. aestivum</i> Kharkov	+	+	—	—	+	+	<i>ne₁Ne₂Ne₃</i>
" Jones Fife	+	+	—	—	+	+	"
" Fulcaster	+	+	—	—	+	+	"
" Blackhull	+	+	—	—	+	+	"
" H ₁₁	+	+	—	—	+	+	"
" Riebesel	+	+	—	—	—	+	"
<i>T. macha subletshchumicum</i>	+	+	+	+	—	—	<i>Ne₁Ne₂ne₃</i>
Synthesized hexaploids							
ABD-III	—	—	—	—	+	+	<i>ne₁ne₂Ne₃</i>
ABD-XII	—	—	—	—	+	+	"
ABD-VI	—	—	+	+	+	+	<i>Ne₁ne₂Ne₃</i>
ABD-VIII	—	—	+	+	+	+	"
ABD-X	—	—	+	+	+	+	"
ABD-I	—	—(L)	+	+	—	+(D)	"
ABD-II	—	—	+	+	—	+	"
ABD-IV	—	—	+	+	—	+	"
ABD-V	—	—	+	+	—	+	"
ABD-VII	—	—	+	+	—	+	"
ABD-IX	—	—(L)	+	+(D)	—	+	"
ABD-XI	—	—	+	+	—	+	"

+: Necrotic. —: Non-necrotic. D: Dwarf. L: Lethal at the tillering stage (Nishikawa's type II necrosis).

* Early observation made at the time of transplantation on Dec. 5, 1961.

** Late observation made at shooting stage on Apr. 26, 1962.

Table 4. Genotypes of some varieties of common wheat and its ancestors

Haploid genotypes	Varieties
Common wheat	
$ne_1ne_2ne_3$	none
$Ne_1ne_2ne_3$	<i>T. macha palaeo.</i>
$ne_1Ne_2ne_3$	none
$ne_1ne_2Ne_3$	<i>T. aestivum</i> Chinese Spring, Marquillo, Trumbull, American Banner, Pawnee, S-615, <i>erythrospermum</i> ; <i>T. compactum</i> 44; <i>T. spelta duha.</i>
$Ne_1Ne_2ne_3$	<i>T. macha sublet.</i>
$Ne_1ne_2Ne_3$	<i>T. aestivum</i> Prelude, Nowinka; <i>T. sphaerococcum</i>
$ne_1Ne_2Ne_3$	<i>T. aestivum</i> Kharkov, Jones Fife, Blackhull, Fulcaster, Riebesel, H ₁₁
Emmer wheat	
ne_1ne_2 —	<i>T. dicoccum</i> Vernal; <i>T. turgidum nigrob.</i>
Ne_1ne_2 —	<i>T. dicoccoides spont.</i> ; <i>T. persicum str.</i> ; <i>T. orientale insigne</i> ; <i>T. durum</i> Gulab, Golden Ball, Pentad, <i>reichenbachii</i> *; <i>T. dicoccum liguliforme</i> *
ne_1Ne_2 —	none
Ne_1Ne_2 —	<i>T. dicoccoides kotschyanum</i> *, <i>straussianum</i> *; <i>T. dicoccum</i> Khapli
<i>Aegilops squarrosa</i>	
— — Ne_3	<i>typica</i> No. 2, Sears'; <i>strangulata</i> KUSE 2112, KUSE 2118, KUSE 2124, KUSE 2135; <i>meyeri</i> KUSE 2144
— — ne_3	none

* Taken from Nishikawa (1962).

Fig. 1. 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 numeral indicates number of varieties having the respective genotype.

strains so far tested have Ne_3 . In common wheat a great majority of varieties are either $ne_1ne_2Ne_3$ or $ne_1Ne_2Ne_3$, each genotype representing more than 40 per cent of the examined total. The third genotype $Ne_1ne_2Ne_3$ is found in about 11 per cent of varieties. A single variety is known having each one of two other genotypes, $Ne_1ne_2ne_3$ and $Ne_1Ne_2ne_3$. No variety was found to be either $Ne_1Ne_2Ne_3$, $ne_1Ne_2ne_3$ or $ne_1ne_2ne_3$.

Discussion

Monosomic analysis of complementary necrosis revealed that three necrosis genes, Ne_1 , Ne_2 and Ne_3 are located in chromosomes 5B (V), 2A (XIII) and 3D (XVI), respectively. This result is in accord with Hermesen's three-gene hypothesis. However, B_1 and F_2 data from the cross *T. macha subletshchumicum* × Chinese Spring indicated that a recessive gene in addition to the above-mentioned must be considered in the expression of necrosis.

Taking the three major genes into consideration, eight genotypes concerning necrosis can be assumed for common wheat varieties. Among them the genotype $Ne_1Ne_2Ne_3$ is lacking due to necrosis. Another genotype, $ne_1ne_2ne_3$ 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.

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 2-major genes in F_2 's. Thick line: necrotic F_1 's and segregation of 3-major genes in F_2 's.

Five of the seven possible genotypes are represented by at least one variety. Their representatives are also indicated in Fig. 2. No variety is known at present

to have the remaining two genotypes, $ne_1ne_2ne_3$ and $ne_1Ne_2ne_3$ but they could be selected in the progeny of the cross between *T. macha subletshchumicum* ($Ne_1Ne_2ne_3$) and Chinese Spring ($ne_1ne_2Ne_3$).

As to the distribution of necrosis genes, there is a similarity in relative frequencies of Ne_3 and ne_3 alleles between common wheat and *Ae. squarrosa*. That is, all *Ae. squarrosa* strain and a great majority of common wheat varieties have Ne_3 . This fact suggests that the *Ae. squarrosa*, which was 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, to have been derived from some other hexaploid species, in which the mutation from Ne_3 to ne_3 occurred. 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 an isolated species among the hexaploids and seems to be out of the main phylogenetic path of common wheat. This finding contradicts Kihara's previous assumption that *T. macha* might have been the progenitor of the other hexaploid species (Kihara 1959).

Two remarkable differences are noticed in the distribution of Ne_1 and Ne_2 at the tetra- and hexaploid levels. First the majority of Emmer varieties have the genotype Ne_1ne_2 , which is found only in a minor fraction of common wheats. Secondly, the gene combination ne_1Ne_2 is found in a large fraction 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. squarrosa* would be lethal due to necrosis. But many cultivated Emmer varieties which are either Ne_1ne_2 or ne_1ne_2 can be put forward as the presumable progenitors, as proposed by Kihara and Lilienfeld (1949). The Ne_1 , ne_1 and 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 ne_1Ne_2 and those of the genotype Ne_1Ne_2 could not have been the donors of the AB genomes to common wheat. These facts are in favor of the hypothesis that Ne_2 of common wheat originated at the hexaploid level rather than having been derived from Emmer wheat. The prevalence of this presumably new allele in common wheat varieties suggests its selective advantage at the hexaploid level. The relative frequencies of Ne_1ne_2 and ne_1ne_2 gene-combinations are reversed in Emmer and common wheats. Since other data of Tsunewaki (1962) indicated rather frequent gene exchanges between tetra- and hexaploid wheats, this shift of the gene frequency also seems to point to a special selective advantage of ne_1 or disadvantage of

Ne_1 at the hexaploid level.

Summary

1) It has been known that complementary necrosis in common wheat is mainly controlled by three genes, Ne_1 located in chromosome 5B (V), Ne_2 in 2A (XIII) and Ne_3 in 3D (XVI). However, the B_1 and F_2 data from the cross *T. macha subletshchumicum* $\times$ *T. aestivum* Chinese Spring indicated that a recessive gene in addition to the above-mentioned genes must be considered regarding the expression of necrosis.

2) Relationships among various varieties of common wheat concerning necrosis are represented in the diagram of Fig. 2.

3) Distribution of the three major genes in common wheat and its ancestors, Emmer wheat and *Ae. squarrosa*, was investigated using *T. aestivum* Prelude ($Ne_1ne_2Ne_3$), *T. aestivum* Kharkov ($ne_1Ne_2Ne_3$) and *T. macha subletshchumicum* ($Ne_1Ne_2ne_3$) as test varieties.

In Emmer wheat a majority of varieties were found to have the genotype Ne_1ne_2 , while minor fractions were either ne_1ne_2 or Ne_1Ne_2 .

All strains of *Ae. squarrosa* so far tested had Ne_3 .

In common wheat, most varieties were either $ne_1ne_2Ne_3$ or $ne_1Ne_2Ne_3$, while a small fraction were $Ne_1ne_2Ne_3$. One variety only was found to be $Ne_1ne_3ne_3$ and another only one to be $Ne_1Ne_3ne_3$, both belonging to *T. macha*.

4) From these results, the genotypes of Emmer wheat, that supplied the AB genomes to common wheat, are assumed to be Ne_1ne_2 or ne_1ne_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 Ne_3 . All strains of *Ae. squarrosa* so far tested had this allele.

5) The presumable hexaploid progenitor must have had either $Ne_1ne_2Ne_3$ or $ne_1ne_2Ne_3$. In common wheat, some forms of *T. spelta*, *T. sphaerococcum*, *T. compactum* and *T. aestivum* have these genotypes. *T. macha*, that is an exception in possessing the 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.

6) It is suggested that Ne_2 in common wheat originated at the hexaploid level rather than to have been derived from Emmer wheat. Possibility of selective advantage of Ne_2 and disadvantage of Ne_1 at the hexaploid level is suggested.

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