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Necrosis and Chlorosis Genes in Common Wheat and its Ancestral Species[1)]

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Both necrosis and chlorosis are classifiable into two types which differ from each other in phenotypic expression as well as in genetic basis (Caldwell and Compton 1943, Nishikawa 1962, Hermsen 1966, Tsunewaki and Hamada 1968). Of these, necrosis type 1 is caused by two complementary genes, Ne_1 on chromosome 5B and Ne_2 on 2B (XIII) (Tsunewaki 1960). Similarly, chlorosis type 1 is caused by complementary genes, Ch_1 on 2A (II) (Zeven unpubl.) and Ch_2 on 3D (Tsunewaki and Kihara 1961).

We investigated geographical as well as taxonomical distribution of these genes using a world-wide collection of tetra- and hexaploid wheats (Tsunewaki and Nakai 1967a, b, c, Tsunewaki and Hori 1967, Tsunewaki et al. 1971). The results obtained, including unpublished data, are compiled in this article.

Materials and Methods

Cultivars or strains of six hexaploid species, *Triticum aestivum*, *T. compactum*, *T. sphaerococcum*, *T. spelta*, *T. vavilovii* and *T. macha*, and those of six tetraploid species, *T. dicoccoides*, *T. dicoccum*, *T. durum*, *T. turgidum*, *T. carthlicum* and *T. timopheevi*, were used. All the hexaploid species have the same genome constitution, AABBDD with 2n=42, while all tetraploids except *T. timopheevi* are AABB with 2n=28, *T. timopheevi* being AAGG, 2n=28.

Cultivars or strains of those species were crossed to three testers, *T. aestivum* cv. Jones Fife (genotype $ne_1Ne_2ch_1Ch_2$), *T. aestivum* cv. Prelude ($Ne_1ne_2ch_1Ch_2$) and *T. macha* var. *subletschchumicum* ($Ne_1ne_2Ch_1ch_2$). Resulting F_1 hybrids were grown in a field to observe the incidence of necrosis and chlorosis. Based on a "necrosis-chlorosis spectrum" for the three F_1 hybrids, the genotype of all tested materials can be determined (Tsunewaki 1966). The genotype is represented in the haploid phase, because wheat is generally homozygous due to a strong tendency for self-fertilization.

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Table 1. Frequencies of various genotypes for necrosis and chlorosis in *T. aestivum* and *T. compactum*

Country or district	Necrosis				Chlorosis			
	No. var. tested	$ne_1\ ne_2$	$Ne_1\ ne_2$	$ne_1\ Ne_2$	No. var. tested	$ch_1\ ch_2$	$Ch_1\ ch_2$	$ch_1\ Ch_2$
Asia (incl. Egypt)								
Japan	195	60%	32%	8%	196	2%	0%	98%
China	168	54	39	7	153	7	0	94
Tibet	17	65	35	0	18	11	0	89
India	51	80	14	6	51	2	0	98
Pakistan	36	94	6	0	36	0	0	100
Afghanistan	37	95	5	0	37	0	0	100
Iran	139	58	42	0	135	0	0	100
Caucasus	143	46	46	8	156	3	0	97
Turkey	63	43	54	3	67	3	0	97
Syria	4	100	0	0	4	0	0	100
Egypt	25	28	80	0	25	0	0	100
Subtotal	878	58.1	36.9	5.0	878	3	0	97
Europe								
Norway	11	100	0	0	13	0	0	100
Sweden	34	100	0	0	35	0	0	100
Finland	15	87	0	13	14	14	0	86
USSR	69	73	16	12	78	14	0	86
Romania	7	100	0	0	9	11	0	89
Bulgaria	24	88	4	8	25	0	0	100
Greece	11	91	0	9	13	15	0	87
Yugosalvia	15	100	0	0	16	0	0	100
Hungary	3	67	0	33	3	0	0	100
Italy	54	72	11	17	57	5	0	95
Spain	123	80	12	8	127	2	0	98
Portugal	19	68	11	21	20	10	0	90
France*	67	51	3	46	-	-	-	-
Germany*	109	42	16	42	-	-	-	-
Netherlands*	33	48	9	42	-	-	-	-
Belgium*	21	38	24	38	-	-	-	-
England*	10	60	0	40	-	-	-	-
Subtotal	625	67.7	9.9	22.4	410	6	0	94
Americas								
Canada	51	78	12	10	50	0	0	100
USA	271	54	12	34	278	5	0	95
Mexico	13	77	23	0	14	0	0	100
Peru	7	71	29	0	13	23	0	77
Chile	7	43	14	43	9	33	0	67
Argentina	24	58	0	42	23	13	0	87
Uruguay	11	100	0	0	16	0	6	94
Brazil	15	13	0	87	16	0	0	100
Subtotal	399	58.1	11.3	30.6	419	5	0	95
Australia	72	79	19	1	69	1	0	99
Grandtotal	1,974	61.9	22.5	15.6	1,776	4.0	0.1	95.9

* Cited from Hermsen (1963)

Results and Discussion

1. *Necrosis genes*

(a) Distribution in *T. aestivum* and *T. compactum*

Results of geographical distribution of the three necrosis genotypes in bread wheat, *T. aestivum* and *T. compactum* are summarized in Table 1 and Fig. 1. In these, Hermsen's data (1963) for five European countries are included, which we had omitted in our investigation to avoid overlapping of research. From the results presented in Table 1, we notice the following facts:

(i) In many Asian countries or districts, i. e. Japan, China, Tibet, Iran, the Caucasus and Turkey as well as in Egypt, Ne_1-carriers are abundantly found, while Ne_2-carriers are

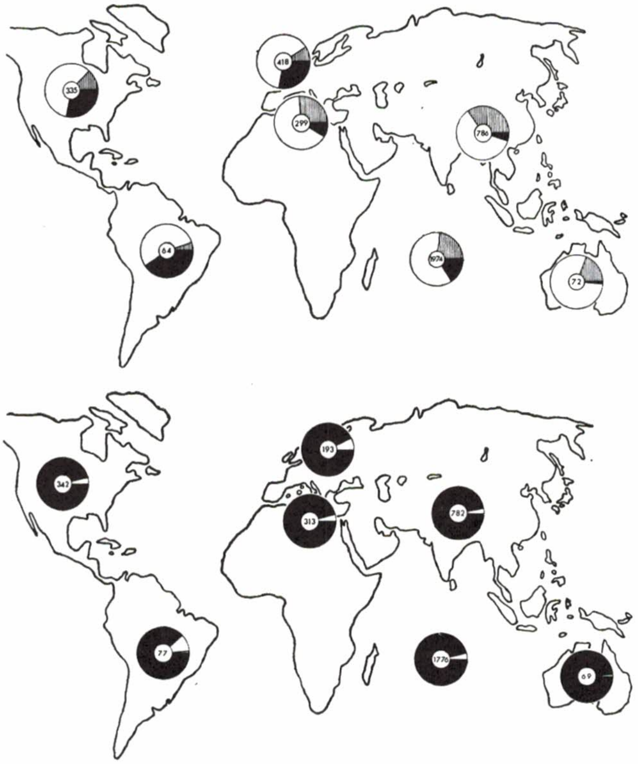

Fig. 1. Relative frequencies of various necrosis and chlorosis genotypes in six geographical populations (Asia, Mediterranean, Europe, North and South Americas, and Australia) of bread wheat, *T. aestivum* and *T. compactum*. (Number of cultivars tested is given in the center of each circle.)
Top: Necrosis genotypes. $Ne_1\,ne_2$ --- shaded, $ne_1\,Ne_2$ --- solid, and $ne_1\,ne_2$ --- blanck.
Lower: Chlorosis genotypes. $Ch_1\,ch_2$ --- shaded, $ch_1\,Ch_2$ --- solid, and $ch_1\,ch_2$ --- blanck.

very rare or totally missing. The northern border of this region is Japan-China-Caucasus-Turkey-Egypt.

(ii) In Western countries, i. e. Germany, France, the Netherlands, Belgium, England, the USA, Chile, Brazil and Argentina, Ne_2-carriers are prevalent, while Ne_1-carriers are rare.

(iii) In a transitional zone between the above two regions, that includes the USSR, the Balkan countries, Italy, Spain and Portugal, the frequencies of both Ne_1- and Ne_2-carriers are relatively low.

(iv) Four local populations of Western countries; those of Canada, Mexico, Peru and Australia, appear to resemble the Asian type.

(v) Some "clean" spots showing a high frequency of non-carriers are found sporadically. These are in Pakistan-Afghanistan, and the Balkan and Scandinavian Peninsulas.

Distribution of the two necrosis genes in two growth habit types was also investigated. Results are summarized in Table 2 and Fig. 2. In Asia, including Egypt, both the spring

Table 2. Frequencies of the three necrosis genotypes in different growth habit types of *T. aestivum* and *T. compactum*

Region	Spring*				Winter			
	No. var. tested	$ne_1\ ne_2$	$Ne_1\ ne_2$	$ne_1\ Ne_2$	No. var. tested	$ne_1\ ne_2$	$Ne_1\ ne_2$	$ne_1\ Ne_2$
Asia								
Japan	67	73%	25%	1%	108	51%	39%	10%
China	90	60	33	7	94	48	45	7
India	51	82	12	6	1	0	100	0
Central Asia	98	78	22	0	118	66	34	0
Turkey	60	45	52	3	3	0	100	0
Syria, Egypt	29	31	69	0	0	-	-	-
Subtotal	395	65	32	3	324	55	40	6
Transitional Zone								
USSR	17	71	24	6	9	78	11	11
Italy	36	61	14	25	25	64	8	28
Iberia	42	81	7	12	63	68	17	14
Subtotal	95	72	13	16	97	68	14	18
North Europe								
	60	97	0	3	0	-	-	-
North America								
Canada	48	83	13	4	3	0	0	100
USA	105	58	28	14	166	52	2	46
Mexico	13	77	23	0	0	-	-	-
Subtotal	166	67	23	10	169	51	2	47
South America								
	19	26	11	63	2	50	0	50
Australia	70	80	20	0	2	50	0	50

* Includes intermediate type.

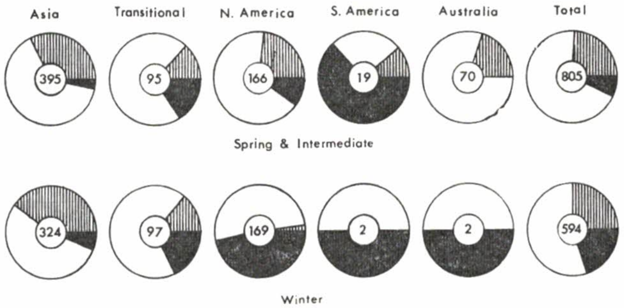

Fig. 2. Relative frequencies of three necrosis genotypes in winter and spring (including intermediate) types of bread wheat, *T. aestivum* and *T. compactum*. ($Ne_1\,ne_2$ --- shaded, ne_1Ne_2 --- solid, $ne_1\,ne_2$ --- blanck)

and winter types contained Ne_1-carriers at high frequencies (30-40 %). In the transitional zone, both growth habit types contained the Ne_1- and Ne_2-carriers in similarly moderate frequencies. The Australian population resembled the Indian wheat in conformity with its breeding history. In North America, however, the two types revealed contrasting population structures, i. e. the spring type resembled the Asian population, containing a relatively large number of Ne_1-carriers. Evidently, man-controlled gene exchanges between the two ecotypes are strongly restricted on this continent. Spring wheat from South America showed a very high frequency of Ne_2-carriers, differing markedly from that of North America. This indicates that there is no appreciable gene exchange between the spring wheats of North and South Americas.

(b) Distribution in other hexaploid species

Distribution of the three necrosis genotypes in *T. macha*, *T. spelta*, *T. vavilovii* and *T. sphaerococcum* was also investigated. These results are also summarized in Table 3 and

Table 3. Frequencies of various genotypes for necrosis and chlorosis in common wheat

Species & population	Necrosis				Chlorosis			
	No. var. tested	$ne_1\,ne_2$	$Ne_1\,ne_2$	$ne_1\,Ne_2$	No. var. tested	$ch_1\,ch_2$	$Ch_1\,ch_2$	$ch_1\,Ch_2$
T. macha								
Asian	13	23%	77%	0%	13	15%	85%	0%
T. spelta, *T. vavilovii*								
Asian	3	0	100	0	3	0	0	100
Western	102	40	0	60	102	3	0	97
T. sphaerococcum								
Asian	2	50	50	0	3	0	0	100
T. aestivum, *T. compactum*								
Asian	878	58	37	5	878	3	0	97
Western*	1,024	64	10	26	829	6	0	94

* European and American populations are included.

Fig. 3. *T. macha* and *T. vavilovii* are endemic to the Caucasus. *T. spelta* occurs in Iran and the alpine regions of Europe. *T. sphaerococcum* is endemic to West Pakistan and the northern part of India.

Asian populations of all the species revealed high frequencies of Ne_1-carriers, while Western populations contained large numbers of Ne_2-carriers. Evidently, hexaploid wheat had differentiated into Asian and Western populations beyond the species level. No simple hypothesis can be offered to explain species differentiation on the one hand and superspecific differentiation into Asian and Western populations on the other. This situation indicates multiple gene introgressions from emmer wheat to common wheat, contributing to speciation in the latter (Tsunewaki 1968).

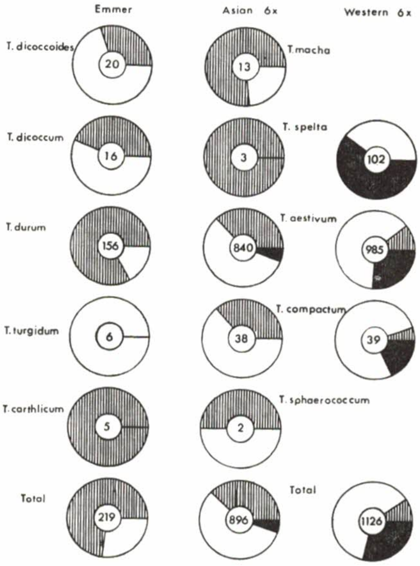

Fig. 3. Relative frequencies of three necrosis genotypes in various species of tetra- and hexaploid wheats. Hexaploids are subdivided to the Asian and Western populations. ($Ne_1 ne_2$ --- shaded, $ne_1 Ne_2$ --- solid, $ne_1 ne_2$ --- blanck)

(c) Distribution in tetraploid species

Frequencies of the three necrosis genotypes in tetraploid wheat were investigated in order to clarify the genetic relationship between tetra- and hexaploid wheats. Results are summarized in Table 4 and Fig. 3. Nishikawa's data (1967) are also included. He analyzed 41 cultivars (or strains) of emmer wheat, including 8

Table 4. Frequencies of various genotypes for necrosis and chlorosis in tetraploid wheats

Species & population	Necrosis				Chlorosis		
	No. var. tested	$ne_1\ ne_2$	$Ne_1\ ne_2$	$ne_1\ Ne_2$	No. var. tested	ch_1	Ch_1
T. dicoccoides	20	70%	30%	0%	27	74%	26%
T. dicoccum	16	56	44	0	17	88	12
T. durum	156	17	83	0	157	100	0
Asia	69	9	91	0	69	100	0
Europe	49	33	67	0	49	100	0
Americas	15	13	87	0	15	100	0
Australia	3	33	67	0	3	100	0
Unknown	20	10	90	0	21	100	0
T. turgidum	6	100	0	0	8	100	0
T. carthlicum	5	0	100	0	5	100	0
Others	16	25	75	0	21	100	0
Total	219	27	73	0	235	96	4
T. timopheevi	2	100	0	0	3	100	0

Note. Nishikawa's data (1967) on necrosis genotypes of 41 emmer varieties are included.

of *T. dicoccoides*, 2 of *T. dicoccum*, 20 of *T. durum*, 2 of *T. turgidum*, 3 of *T. carthlicum* and 6 of other species.

Totally, 73 % of emmer wheat was found to be Ne_1-carriers. The remaining strains were non-carriers. No Ne_2-carriers were found. The frequency of Ne_1-carriers was particularly high in *T. durum* and *T. carthlicum*. *T. durum* cultivars were collected from different parts of the world, as shown in the same table. The frequency of Ne_1-carriers was very high in all local populations. In this species, at least, differentiation into Asian and Western subpopulations, which was found in common wheat, could not be detected. Results presented in Table 1, 3 and 4 indicated that the Ne_2 gene has occurred in common wheat, and that its Asian population is the progenitor type of the Western population.

2. *Chlorosis genes*

(a) Distribution in *T. aestivum* and *T. compactum*

Results of geographical distribution studies of the three chlorosis genotypes in the two species of bread wheat are summarized in Table 1 and Fig. 1. In all parts of the world Ch_2-carriers occupied the great majority of local populations with sporadical occurrence of non-carriers. Only one Ch_1-carrier has been found in Uruguay among the 1,776 cultivars tested. In comparison to the necrosis genes, no geographical differentiation of bread wheat has been found for chlorosis genes.

(b) Distribution in other hexaploid species

Distribution of the three chlorosis genotypes in other hexaploid species is shown in Table 3 and Fig. 4. As in bread wheat, Ch_2-carriers are most common in *T. spelta*, *T. vavilovii* and *T. sphaerococcum* with sporadical occurrence of non-carriers. *T. macha*, however, showed an extremely high frequency of Ch_1-carriers and a complete lack of Ch_2-carriers. As previously stated (Tsunewaki and Kihara 1961, Tsunewaki 1969, 1971), *T. macha* seems to have originated in a different way than the other hexaploid species, and a Ch_1-carrier of

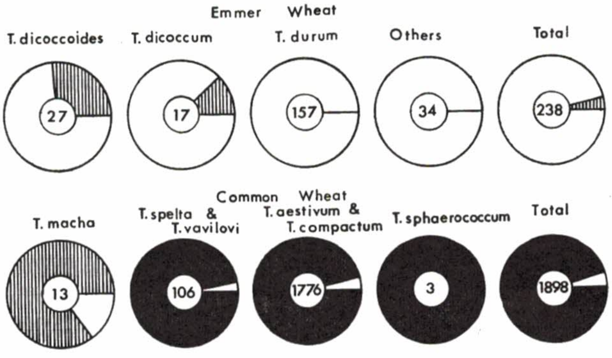

Fig. 4. Relative frequencies of Ch_1-, Ch_2- and non-carriers in various species of tetra- and hexaploid wheats. (Ch_1-carrier --- shaded, Ch_2-carrier --- solid, non-carrier --- blanck)

emmer wheat seems to have been involved in its origin.

(c) Distribution in tetraploid species

Of the two chlorosis genes, only Ch_1, in A genome, should be found in the tetraploid species, because the other gene, Ch_2, is in D genome. Distribution of two chlorosis genotypes, Ch_1-carrier and the non-carrier, in the tetraploid species was studied. Results are shown in Table 4 and Fig. 4. In this table, Nishikawa's data (1967) from 50 emmer cultivars (or strains), 15 of *T. dicoccoides*, 4 of *T. dicoccum*, 19 of *T. durum*, 2 of *T. turgidum*, 3 of *T. carthlicum* and 7 of unclassified, are cited again.

Ch_1-carriers were found in two species, *T. dicoccoides* and *T. dicoccum*, while all other species were monotypic, containing only non-carriers. One of these Ch_1-carrying emmer wheats might have been involved in the origin of *T. macha*.

Conclusion

The above results lead us to the following conclusions:

(1) For necrosis genes, the hexaploid wheat has differentiated into two superspecific populations; Asian and Western types. The Asian type population is the original, from which the Western type arose by acquisition of the Ne_2 gene.

(2) Man-controlled gene exchanges are rather limited between the spring common wheats for North and South America, as well as between the spring and winter common wheats of the North American Continent.

(3) *T. macha* must have a different origin than the other hexaploid species; a Ch_1-carrying emmer wheat is probably involved to its origin.

(4) Because the great majority of emmer wheats carry the Ne_1 gene, the B genome donor of emmer wheat must be an Ne_1-carrier. Investigation of this carrier in Sitopsis section of *Aegilops* will provide additional evidence on the origin of emmer wheat.

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Literature Cited

Caldwell, R.M. and Compton, L.E. 1943. Complementary lethal genes in wheat causing a progressive lethal necrosis of seedlings. J. Hered. **34**: 67–70.

Hermsen, J.G. Th. 1963. Hybrid necrosis as a problem for the wheat breeder. Euphytica **12**: 1–17.

Hermsen, J.G. Th. 1966. Hybrid necrosis and red chlorosis in wheat. Proc. II Int. Wheat Genet., Hereditas Suppl. **2**: 439–452.

NISHIKAWA, K. 1962. Hybrid lethality in crosses between emmer wheats and *Aegilops squarrosa*. III. Gene analysis of Type 2 necrosis. Seiken Zihô **14**: 45–50.

TSUNEWAKI, K. 1960. Monosomic and conventional gene analysis in common wheat. III. Lethality. Jap. J. Genet. **35**: 71–75.

TSUNEWAKI, K. 1966. Gene analysis on chlorosis of the hybrid, *Triticum aestivum* var. Chinese Spring × *T. macha* var. *subletschchumicum*, and its bearing on the genetic basis of necrosis and chlorosis. Jap. J. Genet. **41**: 413–426.

TSUNEWAKI, K. 1969. Origin and phylogenetic differentiation of common wheat revealed by comparative gene analysis. Proc. III Int. Wheat Genet. Symp.: 71–85.

TSUNEWAKI, K. 1971. Distribution of necrosis genes in wheat. V. *Triticum macha, T. spelta* and *T. vavilovii*. Jap. J. Genet. **46**: 93–101.

TSUNEWAKI, K. and HAMADA, J. 1968. A new type of hybrid chlorosis found in tetraploid wheats. Jap. J. Genet. **43**: 279–288.

TSUNEWAKI, K. and HORI, T. 1967. Distribution of necrosis genes in wheat. IV. Common wheat from Australia, Tibet and Northern Europe. Jap. J. Genet. **42**: 245–250.

TSUNEWAKI, K., KASAHARA, F. and FUJITA, T. 1971. *Ibid.* VI. Chinese common wheat. Jap. J. Genet. **46**: 103–107.

TSUNEWAKI, K. and KIHARA, H. 1961. F_1 monosomic analysis of *Triticum macha*. Wheat Inform. Ser. **12**: 1–3.

TSUNEWAKI, K. and NAKAI, Y. 1967a. Distribution of necrosis genes in wheat. I. Common wheat from Central Asia. Can. J. Genet. Cytol. **9**: 69–74.

TSUNEWAKI, K. and NAKAI, Y. 1967b. *Ibid.* II. Japanese local varieties of common wheat. Can. J. Genet. Cytol. **9**: 75–78.

TSUNEWAKI, K. and NAKAI, Y. 1967c. *Ibid.* III. U.S. common wheat. Can. J. Genet. Cytol. **9**: 385–393.