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GENETIC DIVERSITY OF THE CYTOPLASM IN *TRITICUM* AND *AEGILOPS*[1]

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SUMMARY

In order to clarify the genetic diversity of the cytoplasm in *Triticum* and *Aegilops*, cytoplasms of 30 *Triticum* and *Aegilops* species (39 strains in total) were introduced into 12 common wheats belonging to five species. All the alloplasmic lines produced and 12 euplasmic lines as the control were grown in four replications, and their 22 characters were observed. Statistical analysis of the data revealed great genetic differences among the cytoplasms. All the cytoplasms were classified into 16 plasma types by their effects on key characters of wheat as well as by a numerico-taxonomical method. These individual plasma types were compared with their chloroplast genome types which have been revealed by restriction fragment pattern analysis of ctDNA (Ogihara and Tsunewaki 1983). In a few cases, different plasma types corresponded to a single chloroplast genome type, suggesting genetic differentiation among their mitochondrial genomes. Male gametophyte development, heading date and haploid induction are probably influenced by the mitochondrial genome. Maternal lineages of almost all polyploid species are definitely traced back to certain diploids; three exceptions are the cytoplasms of *Ae. crassa* (and relatives), *Ae. ovata* and *Ae. kotschyi* (including *Ae. variabilis*), whose origins must be clarified in future works.

In order to grasp a complete spectrum on the genetic diversity of cytoplasm in *Triticum* and *Aegilops*, cytoplasms of 30 species (39 strains in total) were introduced by repeated backcrosses into 12 cultivars or strains of five common wheat species. A list of the cytoplasms is given in Table 1. The common wheats used as the recipient of alien cytoplasms are *T. aestivum* var. *erythrospermum* (abbrev. Tve, code A), strain P 168 (P168, B), cv. Chinese Spring (CS, C), cv. Norin 26 (N26, D), strain Salmon (Slm, E), cv. Jones Fife (JF, F), cv. Selkirk (Sk, G), cv. S-615 (S615, H), *T. sphaerococcum* var. *rotundatum* (Sphr, I), *T. compactum* cv. No. 44 (Cmp, J), *T. spelta* var. *duhamelianum* (Splt, K), and *T. macha* var. *subletschumicum* (Mch, L), all having the same nuclear genome constitution, AABBDD.

All the alloplasmic lines and 12 euplasmic common wheats as the control were grown in four replications (two plants/replication/line) in the 1981/1982 growing season, and the following 22 characters were observed: variegation in midwinter, dry matter weight, flag leaf length and width, number of internodes over 3 cm, culm diameter at the middle part of second internode, lengths of third to first internodes from the top, plant height, ear length, ear number/plant, spikelet number/ear, awn length (in Tve, P168, N26 and S615), heading date, selfed seed fertility, degrees of anther degeneration, pistillody and other types

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Table 1. Cytoplasms of *Triticum* and *Aegilops* species studied in the present investigation.

Cytoplasm		Cytoplasm donor		No. backcrosses[2)]	Plasma type
Code No.	Source[1)]	Species	Genomes (n)		
01	K	*T. boeoticum*	A	14	A
02	K	*Ae. caudata*	C	34	C
03	K	*Ae. umbellulata*	C^u	22	C^u
04	K	*Ae. squarrosa*	D	12	D
05	K	*Ae. comosa*	M	9	M
06	T	*Ae. heldreichii*	M	7	M
07	N	*Ae. uniaristata*	M^u	11	M^u
08	K	*Ae. speltoides*	S	12	S
09	T	*Ae. aucheri*	S	7	G
10	K	*Ae. sharonensis*	S^1	12	S^1
11	T	*Ae. longissima*	S^1	7	B
12	N	*Ae. bicornis*	S^b	19	S^b
13	N	*Ae. mutica*	Mt	11	Mt
14	T	*Ae. mutica*	Mt	5	Mt^2
15	N	*Ae. speltoides*	S	22	G
21	K	*T. dicoccoides spont.*	AB	11	B
22	K	*T. dicoccum*	AB	15	B
23	K	*T. dicoccoides nudigl.*	AG	12	G
24	N	*T. araraticum*	AG	12	G
25	K	*T. timopheevi*	AG	18	G
26	K	*Ae. triuncialis*	C^uC	13	C^u
27	K	Synthetic *triuncialis*	C^uC	11	C
28	K	*Ae. cylindrica*	CD	11	D
29	K	*Ae. biuncialis*	C^uM^b	12	C^u
30	K	*Ae. columnaris*	C^uM^c	12	C^u
31	K	*Ae. ovata*	C^uM^o	26	M^o
32	K	*Ae. triaristata* 4x	C^uM^t	9	C^u
33	K	*Ae. kotschyi*	C^uS^v	13	S^v
34	K	*Ae. variabilis*	C^uS^v	13	S^v
35	N	*Ae. crassa* 4x	DM^{cr}	9	D^2
36	K	*Ae. ventricosa*	DM^v	11	D
37	T	*Ae. biuncialis*	C^uM^b	7	C^u
38	T	*Ae. triuncialis*	C^uC	8	C
51	N	*T. zhukovskyi*	AAG	13	G
52	K	common wheat	ABD	—	B
53	K	*Ae. juvenalis*	C^uDM^j	11	D^2
54	K	*Ae. triaristata* 6x	$C^uM^tM^{t2}$	12	C^u
55	K	*Ae. crassa* 6x	DD^2M^{cr}	12	D^2
56	K	*Ae. vavilovii*	$DM^{cr}S^p$	11	D^2
57	T	*Ae. triaristata* 6x	$C^uM^tM^{t2}$	7	C^u

[1)] K: Genetics Laboratory, Kyoto University, Japan, N: S. S. Maan, North Dakota State University, U. S. A., T: I. Panayotov, Wheat and Sunflower Institute, Bulgaria.

[2)] Including initial cross

of anther malformation, pollen fertility, and frequencies of haploids and twin seedlings (in Slm and Mch).

The cytoplasms affected all the characters investigated differently, among which selfed seed fertility received most drastic effects from alien cytoplasms. The selfed seed fertility spectra of 40 cytoplasms tested against 12 tester wheats are classified into eight types as shown in Fig. 1. In addition, several cytoplasms exerted clear effects in inducing variegation, growth depression, delayed heading, pistillody or haploid formation. Based on the effects on these key characters, 40 cytoplasms are classified into 16 plasma types as shown in Table 2, in which chloroplast genome types (Ogihara and Tsunewaki 1983) and fraction I protein (Rubisco) large subunit types (Hirai and Tsunewaki 1981) are also shown.

A numerico-taxonomical method was also applied for classifying the cytoplasms based on the data on 20 characters (data on haploidy and twinning are excluded). In this case all data were converted to standardized scores, using the formula, $X/S_{\bar{c}}$, where X is the observed datum of each line on a certain character, and $S_{\bar{c}}$ is the standard deviation of that character among 40 cytoplasms for each nucleus. Then, correlation coefficients were calculated between every pair of cytoplasms using the standardized scores of 20 characters × 12 nuclei combinations. Based on these coefficients, the cytoplasms were clustered by the unweighted pair-group method using arithmetic averages (Sneath and Sokal 1973). The

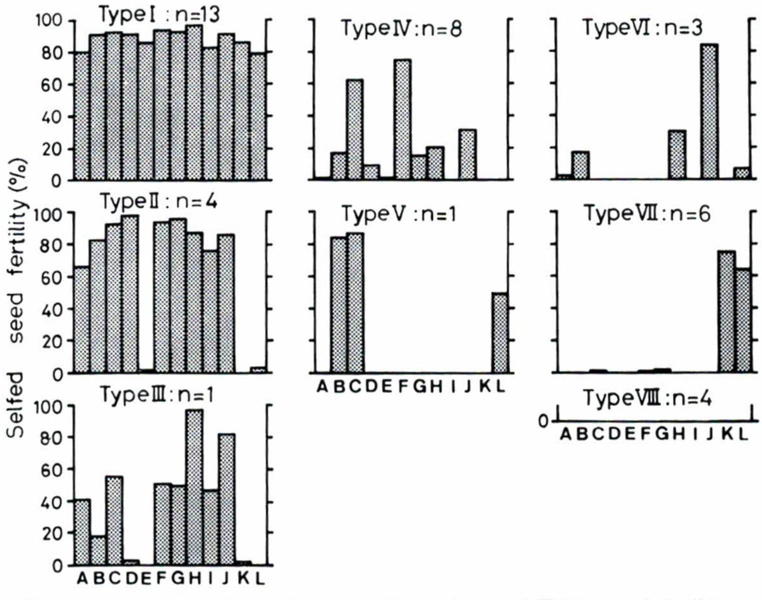

Fig. 1. Fertility spectrum types observed among 40 cytoplasms of *Triticum* and *Aegilops*. Cytoplasms (indicated by code number) belonging to each type are as follows: *Type I*-11, 21, 22, 52 (all B plasma type), 08 (S), 12 (S^b), 04, 28, 36 (D), 35, 53, 55 and 56 (D^2); *Type II*-07 (M^u), 13 (Mt), 33 and 34 (S^v); *Type III*-10 (S^1); *Type IV*-03, 26, 29, 30, 32, 37, 54 and 57 (all C^u); *Type V*-31 (M^o); *Type VI*-02, 27 and 38 (all C); *Type VII*-09, 15, 23, 24, 25 and 51 (all G); and *Type VIII*-01 (A), 05, 06 (M), and 14 (Mt^2).

Table 2. Characteristics of 16 plasma types recognized in *Triticum* and *Aegilops*.

Plasma type	Effect on wheat character						Chloroplast genome[2]	Rubisco LS[3]
	Fertility spect.[1]	Varie-gation	Weakness	Haploidy & twin	Pistillody	Delayed heading		
B	I	−	−	−	−	−	7	H
S	I	−	−	−	−	−	8	H
S^b	I	−	−	−	−	−	1b	L
D	I	−	−	−	−	−	9	L
D^2	I	−	−	−	+	−	1d	L
S^v	II	−	−	+	−	−	1b	L
M^u	II	−	−	+	−	−	10	L
Mt	II	−	−	+	−	++	4	L
S^1	III	−	+	−	−	+	1c	L
C^u	IV	+	+	+	−	+	3	L
M^o	V	−	−	−	−	++	6	L
C	VI	−	−	+	+	−	2	L
G	VII	−	−	−	+	−	5	H
Mt^2	VIII	−	−	+	−	−	4	?
M	VIII	−	+	−	−	+	11a, b	L
A	VIII	+	++	−	−	++	1a	L

[1] Refer to Fig. 1.

[2] After Ogihara and Tsunewaki (1983).

[3] After Hirai and Tsunewaki (1981).

results are shown in a form of dendrogram in Fig. 2, in which the plasma types and some other characteristics of clustered cytoplasms are indicated.

The following 12 plasma type groups are recognized from their effects on key characters as well as from the results of cluster analysis using the data of 20 unselected characters; $(B+S+S^b+D)$: D^2 : (S^v+M^u) : C : G : Mt : Mt^2 : M^o : C^u : S^1 : M : A. On the contrary, B, S, S^b and D types or S^v and M^u types could not be distinguished from their phenotypic effects to wheat characters. However, studies on chloroplast DNA (Ogihara and Tsunewaki 1983) demonstrated that the chloroplast genomes of B, S, S^b and D plasma types are greatly different from each other; this was also true for S^v and M^u plasma types. Thus, we have classified the 40 cytoplasms into 16 plasma types as shown in the last column of Table 1.

Phenotypic effects of two plasma types, S^b and S^v are distinctly different with each other in their ability of inducing male sterility and haploidy, although their chloroplast genomes are identical. Similarly, Mt and Mt^2 plasma types exhibit greatly different effects on male sterility and delayed heading, although their chloroplast genomes are identical. Most likely, their mitochondrial genomes, which seem to concern with male gametophyte development, heading date and haploid formation, differentiated from each other.

Descent of the cytoplasm of most polyploid species can be definitely specified from the present results as follows (cytoplasms are specified with code number in parentheses):

Emmer (21, 22) and common wheat (52) to *Ae. longissima* (11);

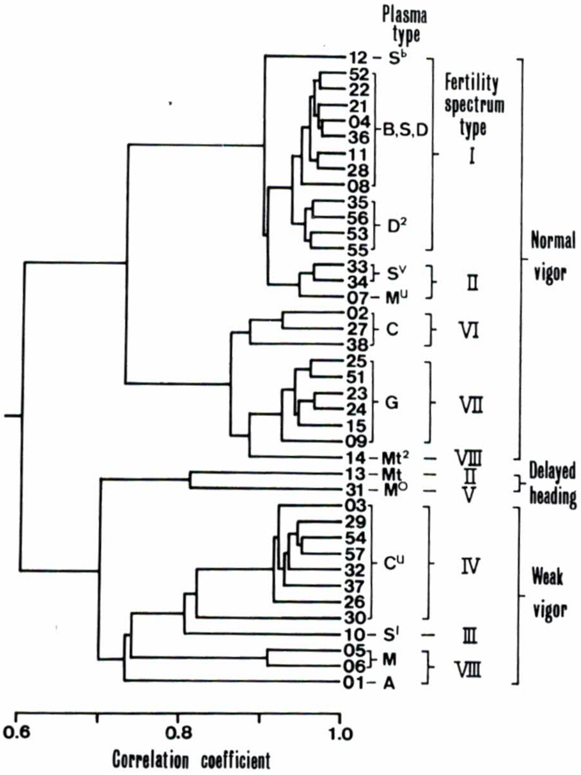

Fig. 2. A dendrogram showing genetic relatedness among 40 cytoplasms of *Triticum* and *Aegilops*; based on the data on 20 characters of NC hybrids of 12 common wheat testers (some other informations are also given in the figure).

Timopheevi wheats (23, 24, 25) and *T. zhukovskyi* (51) to *Ae. aucheri* (09)–*Ae. speltoides* (strain N, 15) complex;

Ae. triuncialis (strain K, 26), *Ae. biuncialis* (29, 37), *Ae. columnaris* (30) and *Ae. triaristata* 4x (32) and 6x (54, 57) to *Ae. umbellulata* (03);

Ae. triuncialis (strain T, 38) and a synthetic *triuncialis* (27) to *Ae. caudata* (02);

Ae. cylindrica (28) and *Ae. ventricosa* (36) to *Ae. squarrosa* (04); and

Ae. juvenalis (53), *Ae. crassa* 6x (55) and *Ae. vavilovii* (56) to *Ae. crassa* 4x (35).

The cytoplasms of *Ae. kotschyi* (33) and *Ae. variabilis* (34) are related to but distinctly different from that of *Ae. bicornis* (12) as to fertility spectrum and haploid induction. No diploid species, whose cytoplasm is closely related to that of *Ae. ovata* (31) or *Ae. crassa* 4x (35) was discovered in the present investigation. The origin of cytoplasm of these polyploid species must be clarified in future investigations.

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