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Genetic Diversity of the Cytoplasm in *Triticum* and *Aegilops*

IV. Distribution of the Cytoplasm Inducing Variegation in Common Wheat*

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Summary. Twelve kinds of common wheat nuclei were placed into the cytoplasms of 23 species of *Aegilops* and *Triticum* by repeated backcrosses in the Laboratory of Genetics, Kyoto University. Using these nucleus-cytoplasm hybrids, the distribution of the variegation-inducing cytoplasms was investigated. The variegation was maternally inherited, and was found to be temperature-dependent; it was expressed only at low temperatures, accompanied by a remarkable reduction in the content of chlorophyll a and b, and recovered to almost normal level in a greenhouse kept at 25 °C. The variegation was expressed only by special combinations of the wheat nuclei and alien cytoplasms; nine common wheat nuclei, Tve, P168, CS, N26, Slm, Sk, S615, Sphr, and Splt, and six cytoplasms, *T. boeoticum*, *Ae. umbellulata*, *Ae. triuncialis*, *Ae. biuncialis*, *Ae. columnaris*, and *Ae. triaristata* 6x, expressed weak to strong variegation in almost all combinations. Combinations of three common wheat nuclei (JF, Comp and Macha) and 17 other cytoplasms showed no variegation: JF, Comp and Macha appeared to have a sort of restoring gene(s) against variegation. Since distribution of the variegation-inducing cytoplasms was confined to the A and C^u type plasmas, it was assumed that the plasmagene(s) responsible for the variegation originated in the diploid level and was transmitted from *Ae. umbellulata* to three tetraploid and one hexaploid species of Polyeides section through the process of amphidiploidization.

Introduction

Following Kihara's work (Kihara 1951, 1959), genetic differences of the cytoplasm among the species of two related genera *Triticum* and *Aegilops* have been studied by many workers (Fukasawa 1953, 1959, Wilson and Ross 1962, Muramatsu 1965, Suemoto 1968, 1973, Maan and Lucken 1971, Maan 1973, and others). These cytoplasmic differences should have arisen by the mutation of plasmagenes in the course of their evolution. In higher plants, plasmagenes are usually transmitted only through the egg cell, i.e., from mother to offspring. These plasmagenes generally interact intimately with certain chromosomal genes and are closely involved in determining the expression of certain characters.

We are investigating the genetic similarity and dissimilarity of the cytoplasm in various species of *Triticum* and *Aegilops*, using their cytoplasm substitution lines with the same common wheat nuclei. In these cytoplasm substitution lines, many phenotypic effects are brought about by novel interactions between the nucleus and alien cytoplasm. For example, male sterility (Kihara 1951), pistillody (Kihara 1951), delayed heading (Fukasawa 1953), depression of plant vigour and occurrence of haploids and twins (Kihara and Tsunewaki 1962) have been reported. Variegation in leaf colour induced by the alien cytoplasm in wheat was first reported by Fukasawa (1953) for *Ae. ovata* cytoplasm. The same phenomenon was reported by Hori and Tsunewaki (1967) for *T. boeoticum* cytoplasm, and by Suemoto (1968, 1973) for the cytoplasms of *T. boeoticum*, *Ae. bicornis*, *Ae. longissima* and *Ae. sharonensis*. The present investigation aimed to clarify the physiological nature of this type of variegation and to reveal the distribution of the variegation-inducing cytoplasm in *Triticum* and *Aegilops* in relation to the phylogeny of the cytoplasm in these genera. The results will be reported in this article.

Materials and Methods

The nuclei of 12 cultivars of common wheat were placed into 23 cytoplasms of *Triticum* and *Aegilops* by repeated backcrosses. The nucleus and cytoplasm donors involved in the cytoplasm substitution work are listed in Table 1. Individual cytoplasm substitution lines are indicated by the name of the cytoplasm donor (in parentheses) connected by a hyphen to that of the nucleus donor. All the cytoplasm substitution lines and their corresponding normal lines of common wheat were planted in an experimental field. The experimental plots were arranged according to a split-plot design with

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Table 1. List of the nucleus and cytoplasm donors used for cytoplasm substitution work

Species	Abbreviation	Genome formula a)	Chromosome no.	Reference b)
(A) Nucleus donor				
Genus *Triticum*				
T. aestivum var. *erythrospermum*	Tve	AABBDD	42	
" " strain P168	P168	"	"	
" " cv. Chinese Spring	CS	"	"	
" " cv. Norin 26	N26	"	"	
" " strain Salmon	Slm	"	"	
" " cv. Jones Fife	JF	"	"	
" " cv. Selkirk	Sk	"	"	
" " cv. S615	S615	"	"	
T. sphaerococcum var. *rotundatum*	Sphr	"	"	
T. compactum cv. No.44	Comp	"	"	
T. spelta var. *duhamelianum*	Splt	"	"	
T. macha var. *subletschchumicum*	Macha	"	"	
(B) Cytoplasm donor				
Genus *Aegilops* Polyeides section				
Ae. umbellulata	*umbellulata*	C^uC^u	14	Muramatsu (1965)
Ae. triuncialis	*triuncialis*	CCC^uC^u	28	Tsunewaki (1973)
Ae. biuncialis	*biuncialis*	$C^uC^uM^bM^b$	28	Sakamoto (unpubl.)
Ae. columnaris	*columnaris*	$C^uC^uM^cM^c$	28	"
Ae. ovata	*ovata*	$C^uC^uM^oM^o$	28	Fukasawa (1953)
Ae. triaristata 6x	*triaristata* 6x	$C^uC^uM^tM^tM^{t2}M^{t2}$	42	Sakamoto (unpubl.)
Ae. kotschyi	*kotschyi*	$C^uC^uS^vS^v$	28	"
Ae. variabilis	*variabilis*	$C^uC^uS^vS^v$	28	"
Genus *Aegilops* Cylindropyrum section				
Ae. caudata	*caudata*	CC	14	Kihara (1951)
Ae. cylindrica	*cylindrica*	CCDD	28	Tsunewaki (1973)
Genus *Aegilops* Sitopsis section				
Ae. speltoides	*speltoides*	SS	14	Tsunewaki (1973)
Ae. sharonensis	*sharonensis*	S^1S^1	14	Sakamoto (unpubl.)
Genus *Aegilops* Vertebrata section				
Ae. squarrosa	*squarrosa*	DD	14	Kihara (1973)
Ae. juvenalis	*juvenalis*	$C^uC^uDDM^jM^j$	42	Sakamoto (unpubl.)
Ae. crassa 6x	*crassa*. 6x	$DDD^2D^2M^{cr}M^{cr}$	42	"
Ae. vavilovii	*vavilovii*	$DDM^{cr}M^{cr}S^pS^p$	42	Otsuka (unpubl.)
Genus *Triticum*				
T. boeoticum	*boeoticum*	AA	14	Tsunewaki (1973)
T. dicoccoides	*dicoccoides*	AABB	28	"
T. dicoccum	*dicoccum*	AABB	28	"
T. dicoccoides var. *nudiglumis*	*nudiglumis*	AAGG	28	Tsunewaki (unpubl.)
T. timopheevi	*timopheevi*	AAGG	28	Wilson & Ross (1962)
T. aestivum	*aestivum*	AABBDD	42	

a) After Kihara and Tanaka (1970)

b) The workers who first introduced the corresponding cytoplasm into common wheat

four replications. In each block, three plants of the same line were planted in a row.

The chlorophyll content was estimated on fresh leaves collected randomly from each replication. They were weighed, ground and pestled using a chilled mortar with cold 80 % acetone and $MgCO_3$. The extract was filtered through a Buchner funnel with a layer of filter paper. The residue was ground and filtered over and over again with acetone until the residue became white and no more pigment could be extracted. Total volume of the extract was measured. The absorption spectrum of the extract was recorded by a Hitachi spectrophotometer using 1 cm cell. The concentrations of chlorophyll a and b were calculated from the following equations, after Maclachlan and Zalik (1963):

$$Ca = \frac{(12.3D_{663} - 0.86D_{645}) \times V}{1000 \times d \times W}$$

$$Cb = \frac{(19.3D_{645} - 3.6D_{663}) \times V}{1000 \times d \times W}$$

Table 2. Maternal inheritance of variegation in (*umbellulata*)-CS. Plants were grown in field and observed at the tillering stage in February

Cross combination		No. of plants	
Maternal parent ×	Paternal parent	Normal	Variegated
Normal CS	× Normal CS	98	0
Normal CS	× (*umbellulata*)-CS	21	0
(*umbellulata*)-CS	× Normal CS	0	52
(*umbellulata*)-CS	× (*umbellulata*)-CS	0	40

where Ca and Cb = content of chlorophyll a and b in mg/g fresh weight, respectively, D = optical density at the indicated wave length, V = volume of extract in ml, d = length of light path in cm, and W = fresh weight of leaves in g. The measurement for each line was repeated four times with different samples.

Results

1. Maternal inheritance of the variegation caused by an alien cytoplasm.

Umbellulata-CS showed typical variegation in midwinter, while normal CS did not variegate at all. Using these lines, inheritance of this character was investigated. The results obtained are shown in Table 2. Undoubtedly, this character is maternally inherited, and is assumed to be under the control of some plasmagene(s).

2. Characteristics of the variegation

Variegation appeared only in some cytoplasm substitution lines from winter to early spring: variegation was induced by the special combinations between wheat nuclei and *Aegilops* or *Triticum* cytoplasms. Of course, none of the *Aegilops* and *Triticum* species show variegation when they have their own cytoplasm. According to Gustafsson's classification (1940), the degree of variegation in these lines falls in the category of *chlorina*, i.e., the leaf becomes uniformly light green and remains yellowish green; or *basiviridis*, i.e., the leaf tip becomes light green, while the base of the leaf blade is yellow.

Variegation began in the tillering stage at the beginning of January. The youngest leaf showed variegation most conspicuously. The lower the temperature, the more remarkable was the variegation; it became most prominent in the later part of February. Variegation continued until the early part of April and disappeared in the middle of this month. When cytoplasm substitution lines which showed variegation in the field were grown in the greenhouse, they did not show variegation throughout all developmental stages. From these results, it became clear that variegation expressed in the cytoplasm substitution lines depends upon temperature.

3. Spectrophotometric determination of chlorophyll content in some cytoplasm substitution lines of CS

In order to find out the relationship between the degree of variegation and the chlorophyll content, the contents of chlorophyll a and b were measured spectrophotometrically in winter and spring, using normal and cytoplasm substitution lines of CS. As shown in Table 3, the chlorophyll content in variegated leaves of (*umbellulata*)-CS fell to about 45 % of that of normal CS in February. The reduction rate was the same for both chlorophylls a and b. (*Biuncialis*)-CS also reduced the chlorophyll content considerably (53 % of normal CS). No significant difference was recognized in other cytoplasm substitution lines. The ratios of chlorophyll a to b in all cytoplasm substitution lines did not change significantly from that of normal CS.

At the beginning of April, the chlorophyll content of (*umbellulata*)- and (*biuncialis*)-CS recovered to some degree (87 % and 80 % of normal CS, respectively), though it was still significantly lower than that of normal CS. In winter the chlorophyll content of (*ovata*)-CS was the same as that of normal CS, whereas it increased slightly in spring ($0.05 < P < 0.1$). The chlorophyll contents of (*speltoides*)-, (*kotschyi*)- and (*variabilis*)-CS did not differ from that of the normal line.

The pattern of seasonal change of the chlorophyll content did not differ significantly between normal CS and (*speltoides*)-, (*kotschyi*)- and (*variabilis*)-CS. In contrast, (*umbellulata*)- and (*biuncialis*)-CS showed a drastic change in chlorophyll content, namely, a remarkable reduction in winter with a great recovery in spring.

The above observations indicate that the expression of variegation induced by the *umbellulata* and *biuncialis*

Table 3. Spectrophotometric determination of chlorophyll content of cytoplasm substitution lines of CS

Line	Variegation	Chlorophyll content (mg/g fr. wt.)			% control	Ratio a/b
		a	b	Total		
Winter (Feb. 16)						
Normal CS	No	1.07	0.35	1.42	100	3.1
(*umbellulata*)-CS	Do	0.48 [b]	0.16 [b]	0.64 [b]	45	3.1
(*speltoides*)-CS	No	0.98	0.33	1.31	92	3.0
(*biuncialis*)-CS	Do	0.54 [b]	0.21 [b]	0.75 [b]	53	2.6
(*ovata*)-CS	No	1.05	0.35	1.39	98	3.0
(*kotschyi*)-CS	No	1.07	0.35	1.42	100	3.1
(*variabilis*)-CS	No	1.00	0.33	1.34	94	3.0
Spring (Apr. 3)						
Normal CS	No	1.21	0.38	1.59	100	3.2
(*umbellulata*)-CS	No	1.05 [a]	0.33 [a]	1.38 [a]	87	3.2
(*speltoides*)-CS	No	1.23	0.39	1.62	102	3.2
(*biuncialis*)-CS	No	0.96 [b]	0.30 [b]	1.27 [b]	80	3.2
(*ovata*)-CS	No	1.35	0.42	1.77	111	3.2
(*kotschyi*)-CS	No	1.09	0.34	1.43	90	3.2
(*variabilis*)-CS	No	1.11	0.36	1.47	92	3.1

[a] and [b]: Significantly different from the normal line at the 5 % and 1 % level, respectively

Table 4. Chlorophyll content of the first and third leaves of the normal and cytoplasm substitution lines of CS grown under two different conditions

Growing condition	Line	First leaves					Third leaves				
		Chlorophyll content (mg/g fr.wt.)			% control	Ratio a/b	Chlorophyll content (mg/g fr.wt.)			% control	Ratio a/b
		a	b	Total			a	b	Total		
Outdoors (March, 5.5 °C on the average)											
	Normal CS (cont.)	0.91	0.31	1.22	100	2.9	1.05	0.32	1.38	100	3.3
	(*umbellulata*)-CS	0.66 [b]	0.20 [b]	0.87 [b]	71	3.3	0.91 [a]	0.29	1.20 [a]	87	3.2
	(*biuncialis*)-CS	0.73 [b]	0.24 [b]	0.97 [b]	80	3.0	0.88 [b]	0.28 [a]	1.16 [b]	84	3.2
	(*ovata*)-CS	0.79 [b]	0.27	1.06 [a]	87	2.9	1.09	0.35	1.44	104	3.2
	(*kotschyi*)-CS	0.88	0.26	1.14	93	3.4	1.13	0.36	1.49	108	3.2
	(*variabilis*)-CS	0.89	0.26	1.15	94	3.4	1.07	0.33	1.40	101	3.2
Greenhouse (25 °C)											
	Normal CS (cont.)	1.10	0.34	1.44	100	3.2	1.03	0.32	1.35	100	3.2
	(*umbellulata*)-CS	1.21	0.38	1.58 [a]	111	3.3	1.22 [b]	0.38 [b]	1.60 [b]	119	3.2
	(*biuncialis*)-CS	1.12	0.36	1.48	103	3.1	1.05	0.31	1.37	101	3.4
	(*ovata*)-CS	1.13	0.37	1.50	104	3.1	1.12	0.35	1.47	109	3.2
	(*kotschyi*)-CS	1.16	0.38	1.54	107	3.1	1.02	0.32	1.34	99	3.2
	(*variabilis*)-CS	1.12	0.37	1.48	103	3.0	0.98	0.30	1.28	95	3.3

[a] and [b]: Significantly different from the normal line at the 5 % and 1 % level, respectively

cytoplasms is probably temperature-dependent. To test this, the seedlings of these cytoplasm substitution lines were grown in March under two different temperature conditions, namely outdoors and in the greenhouse. In Kyoto, seedlings which remained outdoors in March were subjected to low temperature (the average temperature of this month is 5.5 °C), while the greenhouse was kept at a constant temperature of 25 °C. The chlorophyll content of the first and third leaves of seedlings in both groups was measured; the results are shown in Table 4.

When plants were kept outdoors, the *umbellulata* and *biuncialis* cytoplasms decreased chlorophyll content, the decrease being significant at the 1 % or 5 % level. The *ovata* cytoplasm showed a slight decrease only in the first leaves. Two other cytoplasms did not

Table 5. Reaction spectra of the 23 cytoplasms against 12 common wheat nuclei as to the expression of variegation in February in their nucleus-cytoplasm hybrids

Cytoplasm	Tester nucleus											
	Tve	P168	CS	N26	Slm	JF	Sk	S615	Sphr	Comp	Splt	Macha
boeoticum	?	?	++	++	+	?	?	?	?	-	±	?
caudata	-	-	-	-	-	-	-	-	-	-	-	-
umbellulata	±	±	++	++	+	-	+	+	+	-	+	-
squarrosa	-	-	-	-	-	-	-	-	-	-	-	-
speltoides	-	-	-	-	-	-	-	-	-	-	-	-
sharonensis	-	-	-	-	-	-	-	-	-	-	-	?
dicoccoides	-	-	-	-	-	-	-	-	-	-	-	?
dicoccum	-	-	-	-	-	-	-	-	-	-	-	-
nudiglumis	-	-	-	-	-	-	-	-	-	-	-	-
timopheevi	-	-	-	-	-	-	-	-	-	-	-	-
triuncialis	±	±	++	++	+	-	+	±	+	-	+	?
syn-*triuncialis* [a]	-	-	-	-	-	-	-	-	?	-	-	?
cylindrica	-	?	-	-	-	-	-	-	-	-	-	?
biuncialis	±	±	++	++	+	-	+	+	+	-	+	?
columnaris	±	±	+	±	±	-	±	±	+	-	±	-
ovata	-	-	-	-	-	-	-	-	-	-	-	?
kotschyi	-	-	-	-	-	-	-	-	-	-	-	?
variabilis	-	-	-	-	-	-	-	-	-	-	-	?
aestivum	-	-	-	-	-	-	-	-	-	-	-	-
juvenalis	-	-	-	-	-	-	-	-	-	-	-	-
triaristata 6x	-	±	+	+	+	-	+	±	+	-	+	?
crassa 6x	-	-	-	-	-	-	-	-	-	-	-	-
vavilovii	?	?	-	-	?	?	?	?	?	?	?	?

-, ±, + and ++: No, weak, moderate and strong variegation, respectively ?: Not tested

[a] Artificial amphidiploid from the cross, *caudata* (♀) × *umbellulata* (♂)

exhibit any particular effects. In the greenhouse, however, the *umbellulata* cytoplasm significantly increased chlorophyll content. All other cytoplasms did not show any significant effects. In no cases did the a/b ratio change due to alien cytoplasms.

A large difference in chlorophyll content was observed between the greenhouse- and outdoor-grown seedlings of the (*umbellulata*)- and (*biuncialis*)-CS. The chlorophyll content of these lines was conspicuously influenced by temperature: it was decreased at the low temperature but restored by the high temperature. Therefore, the *umbellulata* and *biuncialis* cytoplasms can be considered to be temperature-sensitive cytoplasms as to chlorophyll content. The *ovata*, *kotschyi* and *variabilis* cytoplasms, however, did not show such temperature sensitivity.

4. Distribution of the variegation-inducing cytoplasm

Using the cytoplasm substitution lines of 12 common wheats, which were produced in our laboratory (Tsunewaki 1973, Tsunewaki and Endo 1973, Endo and Tsunewaki 1975, Mukai and Tsunewaki 1975, Tsuji and Tsunewaki 1976, Murata and Tsunewaki 1975), the effects of 23 alien cytoplasms on the expression of variegation in 12 common wheats were investigated; the results are shown in Table 5 in the form of reaction spectra of 23 cytoplasms to the 12 tester nuclei of common wheat. Only six of the 23 cytoplasms tested, i.e., *boeoticum*, *umbellulata*, *triuncialis*, *biuncialis*, *columnaris* and *triaristata* 6x cytoplasms, induced variegation in most of the common wheats used. The degree of variegation in their cytoplasm substitution lines varied with the nuclei involved. In CS and N26 remarkable variegation was induced by the *boeoticum*, *umbellulata* and *biuncialis* cytoplasms. All cytoplasm substitution lines of JF, Comp and Macha did not show any variegation. From these results, it is again clear that the variegation is expressed only in specific combinations of the nucleus and cytoplasm. Three common wheats, JF, Comp and Macha, apparently have some sort of restoring gene against the variegation caused by all the *boeoticum*, *umbellulata*, *triuncialis*, *biuncialis*, and *triaristata* 6x cytoplasms.

The reaction spectra of the *umbellulata*, *triuncialis* and *biuncialis* cytoplasms were almost identical: strong variegation in CS and N26, moderate to weak variegation in Tve, P168, Slm, Sk, S615, Sphr and Splt, and no variegation in JF, Comp and Macha. The

Table 6. Distribution of the variegation-inducing cytoplasm among the eight plasma types found in *Aegilops* and *Triticum* by Tsunewaki *et al.* (in press)

Plasma type	Ploidy level		
	Diploid	Tetraploid	Hexaploid
A	o *T. boeoticum* (A)		
C	× *Ae. caudata* (C)		
C^u	o *Ae. umbellulata* (C^u)	o *Ae. triuncialis* (CC^u) o *Ae. biuncialis* (C^uM^b) o *Ae. columnaris* (C^uM^c)	o *Ae. triaristata* ($C^uM^tM^{t2}$)
D	× *Ae. squarrosa* (D)	× *Ae. cylindrica* (CD)	× *Ae. juvenalis* (C^uDM^j) × *Ae. crassa* (DD^2M^{cr})
G		× *T. dicoccoides* var. *nudiglumis* (AG) × *T. timopheevi* (AG)	
M		× *Ae. ovata* (C^uM^o)	
S	× *Ae. speltoides* (S)	× *Ae. kotschyi* (C^uS^v) × *Ae. variabilis* (C^uS^v) × *T. dicoccoides* (AB) × *T. dicoccum* (AB)	× *T. aestivum* (ABD)
S^1	× *Ae. sharonensis* (S^1)		

o and ×: Carriers and non-carriers of the variegation-inducing cytoplasm, respectively
Note) Genome formula is given in the haploid phase

degree of variegation caused by the *columnaris* and *triaristata* 6x cytoplasms was more or less weaker than that induced by the former three cytoplasms. The reaction spectrum of the *boeoticum* cytoplasm was incomplete and could not be compared satisfactorily with those of the above five cytoplasms, though it is evident that this cytoplasm also causes very strong variegation in some common wheats.

Discussion

The results presented in this paper demonstrate that the variegation is induced by the specific combination of wheat nucleus and alien cytoplasm only at low temperature. Therefore, we can call this type of variegation "conditional variegation". Several workers have already described chlorophyll variegation in tetraploid wheat having some alien cytoplasms. Fukasawa (1957) first reported that *Triticum durum* having the *ovata* cytoplasm showed conspicuous chlorophyll variegation with whitish dots and stripes on the leaves during winter season. He measured chlorophyll content, finding that it was reduced in variegated leaves to about 70 % of that in normal green leaves. From these results, he concluded that the occurrence of variegation was based on the interaction between the *ovata* cytoplasm and the *durum* genome. Hori and Tsunewaki (1967) reported that emmer wheats (*T. turgidum* and *T. dicoccum*) with the *boeoticum* cytoplasm showed chlorophyll variegation at the seedling stage in winter. Suemoto (1968, 1973) reported that *T. turgidum*, with the cytoplasms of *T. boeoticum*, *Ae. longissima*, *Ae. bicornis* or *Ae. sharonensis*, showed variegation in the seedling stage.

The pattern of variegation in common wheat is considerably different from that observed in emmer wheat. The variegated leaf of emmer wheat was characterized by the appearance of yellowish or whitish dots and stripes, but in common wheat by gradual yellowing of the basal part of the leaf.

In other plants, similar cases of maternally inherited leaf colour variegation have been known, *e.g.*, in *Mirabilis* (Correns 1909), in *Antirrhinum* (Baur 1910), in *Nicotiana* (Woods and DuBuy 1951) and so on. However, none of these cases was reported to be temperature sensitive.

The present conditional variegation found in some nucleus-cytoplasm hybrids of wheat will provide an exceptionally useful material for the study of the role of cytoplasm in chlorophyll formation, integration and/or decomposition in the chloroplast.

The present results also demonstrated that some common wheat nuclei have different genotypes as to the expression of the variegation. Undoubtedly, some nuclear genes are involved in this phenomenon. Comparative genetic and biochemical studies of variegation-inducers (*e.g.*, CS and N26) and variegation-suppressors (*e.g.*, JF, Comp and Macha) would provide useful information for the understanding of the nature of interaction between the nucleus and the cytoplasm leading to the expression of variegation.

The cytoplasms of *T. boeoticum*, *Ae. umbellulata*, *Ae. triuncialis*, *Ae. biuncialis*, *Ae. columnaris* and *Ae. triaristata* 6x induced variegation in a large number of common wheats. Tsunewaki *et al.* (in press) classified 21 cytoplasms of *Aegilops* and *Triticum* into eight types, as shown in Table 6, based on their genetic effects on the character expression of common wheat genomes. All cytoplasms belonging to the A and C^u types induced variegation in a large number of common wheats. Endo and Tsunewaki (1975) concluded that the cytoplasm of *Ae. triuncialis* was derived from *Ae. umbellulata*, not from *Ae. caudata*. The cytoplasms of *Ae. biuncialis* and *Ae. columnaris* were assumed to have been derived from *Ae. umbellulata*, not from their M genome donor (Mukai and Tsunewaki 1975).

Besides the *boeoticum* cytoplasm, five variegation-inducing C^u type cytoplasms seem to have common plasmagne(s) for the variegation in accord with the hypotheses of those authors on the origin of the C^u type plasma. Thus, we may assume that the plasmagene(s) that controls variegation was transmitted from a diploid species, *Ae. umbellulata*, to three tetraploid (*Ae. triuncialis*, *Ae. biuncialis* and *Ae. columnaris*) and one hexaploid (*Ae. triaristata*) species through the process of amphidiploidization. In other words, the plasmagene(s) responsible for the variegation occurred at the diploid level and was transmitted to tetra- and hexaploid levels through amphidiploidization.

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