Increasing Genetic Variability in Common Wheat by Utilizing Alien Cytoplasms—Effects of Four *Aegilops* Cytoplasms on the Genetic Variability of the F₃ Generation of the Cross, Norin 26×Norin 61¹⁾

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Cytoplasmic effects of the four *Aegilops* species, i.e., *Ae. squarrosa*, *Ae. kotschyi*, *Ae. speltoides* and *Ae. longissima*, on the genetic variability of agronomic characters of wheat were investigated using a total of 460 F₃ lines which were randomly derived from the cross combinations of allo- and euplasmic Norin 26 with euplasmic Norin 61. It was observed, coincidentally with the trend observed in the F₂ populations (TSUNEWAKI et al. 1985), that cytoplasm of *Ae. kotschyi* caused the most prominent effect. The cytoplasm increased, statistically significantly and/or consistently with the F₂ result, the genetic variability of the seven out of ten characters examined. Cytoplasm of *Ae. speltoides* showed the second most appreciable effect, enlarging the genetic variability of the length of internodes, culm and spike. Cytoplasmic effects of *Ae. squarrosa* and *Ae. longissima* were neither distinct nor desirable. The principal component analysis revealed that none of the alien cytoplasms tested substantially modified the phase or structure of character association, though they more or less changed the genetic variability of individual characters. Cytoplasms with a larger genetic distance from wheat cytoplasm (TSUNEWAKI 1980) caused a wider range of effects, suggesting that new and desirable nucleo-cytoplasmic interactions may occur in a combination of relatively distantly related cytoplasmic and nuclear genomes rather than closely related ones.

KEY WORDS : Alloplasmic line, nucleo-cytoplasmic hybrid, alloplasmic cross combination, *Aegilops* cytoplasm, genetic variability, common wheat.

Introduction

It has been confirmed that a large genetic variation exists in the cytoplasms of *Triticum* and *Aegilops* species (TSUNEWAKI 1980). Exploring the utility of this cytoplasmic variation is one of the most prospective ways to break the productivity ceiling of wheat cultivars today.

One of the main research lines of this aim has been development of promising nucleo-cytoplasmic hybrids by combining nuclear genotypes of existing wheat cultivars with alien cytoplasms (KIYHARA 1979), and many nucleo-cytoplasmic hybrids have been raised and tested until now (HORI and TSUNEWAKI 1969, MAAN and LUCKEN 1971, PANAYOTOV and GOTSOV 1976). The results, however, are rather discouraging ; none of existing wheat genotypes were so well compatible with alien cytoplasms as to give rise to new lines with a substantially advanced productivity, while some *Aegilops* cytoplasms have been suggested to be useful for improving seed quality and disease resistance

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of current wheat cultivars (WASHINGTON and MAAN 1974, KOFOID and MAAN 1982).

Creating new wheat genotypes that interact desirably with some alien cytoplasm is then another possibility to be tried. Only a few experiments have been carried out until now on this line (MAAN *et al.* 1981, KONZAK and ALLAN 1984). The present authors have been conducting a series of experiments on the segregating generations of the cross combinations between alloplasmic (*Aegilops*) and euplasmic wheat cultivar lines, aiming to find out the *Aegilops* cytoplasms which have the potentiality of expanding the genetic variability to segregate new desirable nucleo-cytoplasmic combinations.

Our previously reported observations on the cross combinations between five alloplasmic lines of Norin 26 and euplasmic Norin 61 have shown that the F_2 populations which are alloplasmic for *Ae. kotschy* and *Ae. speltoides* cytoplasms exhibited an increased genetic variability for some agronomic characters (TSUNEWAKI *et al.* 1985). The genetic variation and association of characters in the F_3 generation are investigated in the present paper to derive some additional or confirmative trends.

Materials and Method

Cytoplasmic effects of the four *Aegilops* species, *Ae. squarrosa*, *Ae. kotschy*, *Ae. speltoides* and *Ae. longissima* were studied regarding the genetic variation of the F_3 lines which were randomly derived from the cross combinations between alloplasmic lines of cv. Norin 26 (Norin 26 carrying *Aegilops* cytoplasms) and euplasmic cv. Norin 61. The alloplasmic lines of Norin 26 were produced by repeated backcrosses of Norin 26 to the alloplasmic lines of Chinese Spring; nine backcrosses for *squarrosa* and *kotschy* cytoplasms, ten for *speltoides* cytoplasm, and five for *longissima* cytoplasm. The detailed pedigrees of the alloplasmic lines of Norin 26 were presented in the previous paper of this series (TSUNEWAKI *et al.* 1985).

Ten cross combinations as shown in Table 1 were tested, reciprocal crosses of euplasmic Norin 26 and Norin 61 being included as the check. Six parental lines, i.e., the four alloplasmic lines of Norin 26, euplasmic Norin 26 and Norin 61 were also grown.

Table 1. Cross combinations of the F_3 lines investigated

Cross combination ¹⁾	Cytoplasm (Plasma type)	Number of F_3 lines tested	Year of experiment
(<i>squarrosa</i>)-N 26 × N 61	<i>Ae. squarrosa</i> (D)	50	1982
Reciprocal	<i>T. aestivum</i> (B)	50	"
(<i>kotschy</i>)-N 26 × N 61	<i>Ae. kotschy</i> (S ^v)	50	"
Reciprocal	<i>T. aestivum</i> (B)	50	"
(<i>speltoides</i>)-N 26 × N 61	<i>Ae. speltoides</i> (S)	30	1983
Reciprocal	<i>T. aestivum</i> (B)	30	"
(<i>longissima</i>) N 26 × N 61	<i>Ae. longissima</i> (B)	30	"
Reciprocal	<i>T. aestivum</i> (B)	30	"
N 26 × N 61	"	50, 20 ²⁾	1982, 1983
Reciprocal	"	50, 20	"

¹⁾ N 26=euplasmic Norin 26, N 61=euplasmic Norin 61, (*squarrosa*)-N 26=Norin 26 carrying *Ae. squarrosa* cytoplasm, etc.

²⁾ 50 lines in 1982, and 20 lines in 1983.

The genetic effects of the *Aegilops* cytoplasms may be detected by the comparison between reciprocal crosses. Experiments for *Ae. squarrosa* and *Ae. kotschyi* and those for *Ae. speltoides* and *Ae. longissima* were carried out in two different years, 1982 and 1983. Cross combinations for *Ae. vavilovii* which were included in the F_1 and F_2 experiments previously reported, were not tested in the present F_3 experiment due to technical limitations. Unusually cold and rainy weather of 1982 largely suppressed the growth of wheat plants.

Thirty to fifty F_3 lines for one cross combination were randomly derived from F_2 plants grown in one of the four replicate blocks of the previous experiment (TSUNEWAKI *et al.* 1985). These F_3 lines were sown and transplanted in autumn with the conventional cultivating procedures of the laboratory of Plant Breeding of Kyoto University, being measured in the following spring. These lines were allocated in a split-plot design with two replications; the reciprocal crosses were allocated in pairs to main plots, F_3 lines in the paired reciprocal crosses and parental lines being arranged randomly to sub-plots within a main plot. In each main plot, 15 seedlings per F_3 line were planted 10 cm apart each other in a single row plot with 30 cm distance between neighbouring rows. Several row plots were randomly assigned to each of the two parental lines. Two plants at the verges of each plot row were discarded in taking measurements.

Measurements were taken on individual plant basis for nine characters; heading date (in April, abbreviated as HD), flag leaf length (FL), ear length (EL), ear weight (EW), ears per plant (EN), culm length (CL), lengths of the first, second and third internodes (1I, 2I and 3I, respectively). The ratio 1I/CL was calculated as a variable related to the plant type.

Cytoplasmic effects of the *Aegilops* species were investigated for the variance and correlation of characters which were calculated based on the mean values of the F_3 lines over the two replicate blocks. Since environmental error effect is expected to be largely offset in the mean values of the F_3 line, the phenotypic variance and correlation thus calculated may safely be regarded as genetic ones. Occurrence of transgressive lines for each of the measured characters was also examined. Correlation between F_2 plants and F_3 lines, which may be treated as a realized heritability, was computed to observe the influence of the *Aegilops* cytoplasms on the actually heritable fraction of the F_2 genetic variation. The F_2 data of the previously reported experiment (TSUNEWAKI *et al.* 1985) were used for calculating the F_2 - F_3 correlation. Modification of character association due to the alien cytoplasms was studied by the principal component analysis.

Results

Four statistics, i.e., mean, range (minimum and maximum), variance of the F_3 lines, and heritability estimated from the correlation between F_2 plants and F_3 lines were calculated for each cross combination, and were presented in Table 2.

The statistics of 1982 and 1983 showed a large difference due to the poor weather in 1982. In some characters, the statistics of the check crosses differed largely between reciprocals in reversed order in the two years. This suggests that sampling error

Table 2. (1) Statistics calculated on F₃ line mean basis for each cross combination

Cross combination	heading date (in April)					Flag leaf length (cm)				
	Mean	Min.	Max.	Var. ¹⁾	Her. ²⁾	Mean	Min.	Max.	Var.	Her.
(<i>sqr</i>)-N 26×N 61	25.50	23.76	27.92	0.576	0.222	18.48	14.54	21.34	2.286	0.393
Reciprocal	24.52	21.88	28.07	1.023**	0.408	18.21	14.64	22.63	2.036	0.243
(<i>kts</i>)-N 26×N 61	25.09	22.38	27.03	0.221**	0.308	18.63	15.54	21.36	1.944	0.263
Reciprocal	25.47	23.52	27.00	0.701*	0.474	18.22	15.63	20.81	1.373	0.039
N 26×N 61	25.64	23.85	27.45	0.516	0.357	17.76	15.56	22.68	2.010	0.112
Reciprocal	25.43	23.93	26.54	0.348	0.441	17.62	15.43	21.78	1.885	0.236
(<i>spl</i>)-N 26×N 61	17.46	15.76	19.94	1.201	0.414	22.62	18.98	24.97	2.566	0.128
Reciprocal	17.53	15.29	20.83	2.157*	0.558	21.94	17.84	26.45	3.725	-0.065
(<i>lng</i>)-N 26×N 61	17.01	15.37	19.13	1.081	0.642	22.49	18.60	28.20	6.305*	0.194
Reciprocal	16.82	14.48	19.41	1.528	0.333	22.21	18.41	26.06	2.929	0.096
N 26×N 61	16.64	13.80	18.81	1.246	0.131	22.88	19.16	26.09	3.541	-0.239
Reciprocal	16.22	13.39	17.58	1.033	0.426	22.38	20.14	27.15	2.753	-0.206

Table 2. (2)

Cross combination	Ear length (cm)					Ear weight (g)				
	Mean	Min.	Max.	Var.	Her.	Mean	Min.	Max.	Var.	Her.
(<i>sqr</i>)-N 26×N 61	8.25	7.38	9.29	0.257	0.584	2.23	1.94	2.63	0.029	-0.030
Reciprocal	8.30	7.18	9.99	0.378	0.740	2.22	1.44	2.57	0.044	0.174
(<i>kts</i>)-N 26×N 61	7.98*	6.74	9.54	0.316	0.772	2.12	1.69	2.48	0.037	0.252
Reciprocal	8.12	6.83	9.30	0.272	0.743	2.35	1.69	2.76	0.039	0.161
N 26×N 61	8.21	7.03	9.39	0.313	0.771	2.34	1.98	2.71	0.036	0.332
Reciprocal	8.35	7.09	9.32	0.242	0.618	2.33	1.85	2.74	0.031	0.295
(<i>spl</i>)-N 26×N 61	9.49	8.10	11.87	0.615	0.740	2.42	1.80	3.09	0.097	0.076
Reciprocal	9.66	8.16	10.93	0.526	0.490	2.55	2.05	2.95	0.064	0.046
(<i>lng</i>)-N 26×N 61	10.01	9.00	10.85	0.326	0.374	2.58	1.95	3.25	0.093	-0.114
Reciprocal	9.91	8.84	11.16	0.401	0.618	2.50	2.13	3.32	0.066	-0.009
N 26×N 61	10.07	9.04	11.34	0.529	0.437	2.52	1.95	2.90	0.066	-0.210
Reciprocal	9.83	8.41	11.56	0.552	0.730	2.52	2.04	3.20	0.073	0.089

Table 2. (3)

Cross combination	Ear number					Culm length (cm)				
	Mean	Min.	Max.	Var.	Her.	Mean	Min.	Max.	Var.	Her.
(<i>sqr</i>)-N 26×N 61	4.56	3.13	6.12	0.472	0.207	69.36	48.10	88.07	84.671	0.510**
Reciprocal	4.83	3.76	7.33	0.529	0.019	70.63	47.11	88.75	105.063	0.931
(<i>kts</i>)-N 26×N 61	4.99	3.35	6.65	0.568	0.113	68.79	43.55	91.22	158.417*	0.939
Reciprocal	5.19	3.65	6.63	0.455	-0.129	67.23	46.13	87.43	106.041	0.670**
N 26×N 61	5.05	3.75	7.35	0.527	-0.008	69.55	48.12	85.15	101.777	0.926
Reciprocal	4.90	3.72	6.72	0.531	-0.042	66.06	45.22	89.93	96.029	0.901
(<i>spl</i>)-N 26×N 61	7.96	5.83	11.33	1.815	0.230	73.07	51.52	94.90	111.184	0.873
Reciprocal	7.91	4.33	11.36	2.254	0.150	80.96	64.88	99.47	66.994*	0.626*
(<i>lng</i>)-N 26×N 61	7.95	6.11	11.20	1.721	0.354	76.27	49.80	94.18	160.884	0.840
Reciprocal	8.76	5.70	11.75	2.720	0.336	77.48	62.71	100.00	99.477	0.848
N 26×N 61	8.31	6.09	12.38	2.628	-0.214	80.50	63.25	96.80	98.594	0.916
Reciprocal	8.30	6.80	9.73	0.908	0.257	74.52	48.90	98.43	170.578	0.920

Table 2. (4)

Cross combination	First internode length (cm)					Second internode length (cm)				
	Mean	Min.	Max.	Var.	Her.	Mean	Min.	Max.	Var.	Her.
(<i>sqr</i>)-N 26×N 61	29.60	19.28	37.39	16.773	0.802	20.26	15.06	25.66	6.123	0.827
Reciprocal	28.79	18.81	35.65	17.178	0.792	20.28	13.86	24.75	7.303	0.920
(<i>kts</i>)-N 26×N 61	29.45	18.55	39.09	28.377*	0.926*	20.01	19.74	25.43	11.226*	0.919
Reciprocal	28.03	18.84	39.31	20.296	0.848	19.74	13.77	24.66	7.498	0.849
N 26×N 61	28.58	18.69	35.69	15.858	0.796	20.28	14.54	24.48	7.297	0.860
Reciprocal	27.25	18.07	36.05	17.078	0.847	19.48	14.46	25.16	6.032	0.906
(<i>spl</i>)-N 26×N 61	30.39	21.79	38.04	18.825	0.684	21.31	15.12	27.42	10.010	0.848*
Reciprocal	32.27	24.16	42.91	21.183	0.713	23.35	18.98	28.08	5.366	0.665**
(<i>lng</i>)-N 26×N 61	30.81	18.76	39.61	35.491	0.833	22.03	14.28	27.93	15.139	0.886*
Reciprocal	31.24	22.96	39.85	20.224	0.675	22.02	18.22	28.01	9.132	0.845*
N 26×N 61	31.28	25.25	39.07	16.380	0.533	22.80	17.58	27.32	8.650	0.955
Reciprocal	29.24	20.35	38.43	25.633	0.952	21.00	14.16	28.13	14.684	0.960

Table 2. (5)

Cross combination	Third internode length (cm)					1 I/CL				
	Mean	Min.	Max.	Var.	Her.	Mean	Min.	Max.	Var.	Her.
(<i>sqr</i>)-N 26×N 61	12.98	9.05	16.60	3.106	0.682	0.43	0.38	0.49	0.0006**	-0.086
Reciprocal	13.35	9.18	17.72	3.610	0.754	0.41	0.38	0.44	0.0002	0.356
(<i>kts</i>)-N 26×N 61	12.83	8.46	16.94	4.313	0.787	0.43	0.39	0.48	0.0004	0.263
Reciprocal	12.82	8.92	15.65	3.164	0.826	0.42	0.38	0.49	0.0005	-0.223
N 26×N 61	13.26	9.76	16.46	3.540	0.706	0.41	0.38	0.47	0.0003	0.173
Reciprocal	12.87	8.64	17.15	3.102	0.768	0.41	0.37	0.45	0.0003	0.538
(<i>spl</i>)-N 26×N 61	13.20	9.28	16.99	3.709	0.626	0.42	0.35	0.55	0.0019	-0.066
Reciprocal	14.76	11.31	18.74	2.556*	0.305*	0.40	0.33	0.58	0.0024	0.133
(<i>lng</i>)-N 26×N 61	13.99	9.34	17.47	4.937	0.660	0.40	0.33	0.48	0.0011	0.250
Reciprocal	14.19	11.59	18.01	3.362	0.575	0.41	0.33	0.48	0.0014	-0.112
N 26×N 61	14.86	11.88	19.09	4.091	0.670	0.39	0.34	0.46	0.0014	-0.179
Reciprocal	13.74	8.59	17.84	6.023	0.754	0.40	0.35	0.49	0.0012	0.445

¹⁾ : Variance of F₃ line means.

²⁾ : Heritability estimated by the correlation between F₂ plants and F₃ lines.

*,** : Significantly different from the check cross combinations of euplasmic Norin 26 and Norin 61 at the 0.05 and 0.01 levels, respectively.

in genotypic constitution and interaction of nuclear and cytoplasmic genes with environment (year) may largely be involved, which, however, cannot explicitly be estimated with the design of this experiment. In this situation, test of statistical significance for reciprocal differences is not reliable enough to detect cytoplasmic effects. Coincidence of the present results with the F₂ ones was then taken into account as another criterion; reciprocal differences are likely to be true if observed repeatedly in the F₂ and F₃ generations.

Cytoplasmic modification of mean value was very rarely observed. Statistically significant difference occurred only for ear length of the cross combination (*kotschyi*)-N 26×N 61; the mean value 7.98 of this cross combination is significantly smaller than

Table 3. (1) Summarised representation of the effects of *Aegilops* cytoplasms on the variability of F₃ lines

Cross combination	HD			FL			EL			EW			EN		
	Transg.	Var.	Her.	Transg.	Var.	Her.	Transg.	Var.	Her.	Transg.	Var.	Her.	Transg.	Var.	Her.
(<i>sqr</i>)-N 26 × N 61	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Reciprocal	-	+	+	-	-	-	+	-	-	-	-	-	-	-	-
(<i>kts</i>)-N 26 × N 61	-	+	+	-	+	+	+	+	+	-	-	+	-	-	-
Reciprocal	-	+	+	-	+	+	+	+	+	+	+	-	-	-	-
(<i>spl</i>)-N 26 × N 61	+	+	+	-	-	-	+	+	+	-	-	-	-	-	-
Reciprocal	+	+	+	-	-	-	+	+	+	-	-	-	-	-	-
(<i>lng</i>)-N 26 × N 61	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Reciprocal	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

Table 3. (2)

Cross combination	CL			1I			2I			3I			1I/CL		
	Transg.	Var.	Her.	Transg.	Var.	Her.	Transg.	Var.	Her.	Transg.	Var.	Her.	Transg.	Var.	Her.
(<i>sqr</i>)-N 26 × N 61	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+
Reciprocal	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+
(<i>kts</i>)-N 26 × N 61	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Reciprocal	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
(<i>spl</i>)-N 26 × N 61	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Reciprocal	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
(<i>lng</i>)-N 26 × N 61	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Reciprocal	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Signs +, - and +- under the column 'Transg.' show the occurrence of positive, negative and both types of transgressive lines, respectively. Signs + and ++ (- and --) under the columns 'Var.' and 'Her.' indicate significant increase (decrease) from the check cross combinations of euplasmic Norin 26 and Norin 61, at the 0.05 and 0.01 levels, respectively. Squares of broken line represent the reciprocal differences which are consistent with the F₂ results (TSUNEWAKI *et al.* 1985). Signs + and - attached at the upper right corner of the square indicate that the alloplasmic cross combination showed a larger and smaller value than the euplasmic reciprocal, respectively.

the means of the reciprocal (8.12) and check cross combinations of euplasmic Norin 26 and Norin 61 (8.21 and 8.35). The reduction of ear length by *kotschyi* cytoplasm is consistent with the results of the F_2 population (TSUNEWAKI *et al.* 1985). The effect of *speltoides* cytoplasm of shortening internode length of F_2 population was observed also in this experiment, though not statistically significant.

Results for the occurrence of transgressive lines, variance and heritability were summarised in Table 3, where significant deviations from the check cross combinations of euplasmic Norin 26 and Norin 61 were symbolically shown. Coincidence with the F_2 results was also described in this table.

Cytoplasm of *Ae. kotschyi* showed the most prominent effect in Table 3. The cross combination (*kotschyi*)-N 26 $\times$ N 61 produced a significant increase in the genetic variability and heritability compared to the reciprocal, or, the same change as observed in the F_2 , for the seven out of ten characters examined. It may be suggestive from practical point of view that *kotschyi* cytoplasm expanded the genetic variability of heading date without apparent mal-modification of yield-related characters such as leaf and ear size.

Cytoplasm of *Ae. speltoides* caused the second most remarkable result. Significance test among the F_3 lines and comparison with the F_2 data revealed that the cross combination (*speltoides*)-N 26 $\times$ N 61 has larger genetic variation and heritability than the reciprocal for the four out of ten characters, i.e., ear length, culm length, the second and third internode length. *Speltoides* cytoplasm seems to work mainly on length characters.

Results of the remaining two *Aegilops* cytoplasm are less conspicuous and consistent. For *squarrosa* cytoplasm, difference between the reciprocals was found only for heading date and ear length, genetic variation of these characters being narrowed rather than expanded by *squarrosa* cytoplasm. The influence of *longissima* cytoplasm was observed for the four characters, flag leaf length, ear length, ear weight and number. Cytoplasm of *Ae. longissima* caused different effects to different characters; it increased the genetic variability of flag leaf length, ear weight and ear number, but decreased the variation of ear length.

A number of cases in Table 3 demonstrate that both of paired reciprocal crosses exhibited similar deviations from the check crosses between euplasmic Norin 26 and Norin 61. This phenomenon occurred in all of the four reciprocal pairs tested, but in different ways in different reciprocal pairs. In the pair of (*squarrosa*)-N 26 $\times$ Norin 61 and its reciprocal, for instance, similar transgressant lines were observed for heading date, flag leaf length and ear number, whereas both of the reciprocal crosses of (*kotschyi*)-N 26 and Norin 61 released similar transgressants for heading date, ear number, the first internode length and ratio of the first internode to culm length. The variance of heading date was significantly increased in both reciprocals of (*kotschyi*)-N 26 and Norin 61. The concurrent changes of the reciprocals strongly suggest that some nuclear genes of *Aegilops* species and/or Chinese Spring (cf. TSUNEWAKI *et al.* 1985) remained unsubstituted in the alloplasmic parental lines used in this experiment.

Correlations between characters were calculated for each cross combination to find

out cytoplasmic effects on the association of characters. Among 360 correlations (45 character combinations $\times$ 8 cross combinations), only 12 as shown in Table 4 were significantly different from the reciprocal and/or check crosses of euplasmic Norin 26 and 61. None of these significant deviations were very drastic; the correlations of HD-EW, FL-EW, EL-EW and 1I-1I/CL remained around or below 0.6, those of EN-CL, EN-2I and EN-3I became negative (reversed from the check crosses) but not much intensified, and those of CL-2I and CL-3I remained very high. In addition, seven out of the ten significant deviations from the check cross occurred in the cross combinations carrying wheat cytoplasm.

It is then concluded that the *Aegilops* cytoplasms tested in this experiment caused no essential modification in the structure of character association, while largely or slightly affected the genetic variability of individual characters.

The principal components of the character variation were extracted from the correlation matrix of the characters in order to substantiate the above inference. Eigenvectors of the first and second principal components are presented in Table 5. This table shows that the eigenvectors are essentially the same over all cross combinations, although some modifications presumably due to the difference in experimental conditions are perceived. The first principal component in any cross combination seems to be mainly determined by the four length characters, culm length, lengths of the first, second and third internodes, indicating that lines with a larger plant size tend to have a larger score of this component. The second component, on the other hand, is largely affected by ear characters (EL, EW and EN in 1982, and EL and EW in 1983) and, in a reversed way, by the ratio 1I/CL. This component appears to describe the variation in shape rather than size characters. It then may be said that the main structure of character association remained unchanged over the four *Aegilops* cytoplasms.

Discussion and Conclusion

Results of the present experiment combining with the previous ones for the F_2 (TSUNEWAKI *et al.* 1985) lead to the conclusion that cytoplasm of *Ae. kotschyi* has the largest potentiality of expanding genetic variability of wheat genotypes. The increased variability of heading date without apparent deleterious effects to other yield-related characters would be of great implication for wheat breeding in Japan, where earliness with a moderate or higher level of productivity is required for creating a new cultivar. Yield trial of some promising lines carrying *kotschyi* cytoplasm remains to be carried out in later generations. Cytoplasm of *Ae. speltoides* also increased variation of some characters, especially length characters such as ear length and culm length.

Application of cytoplasm of *Ae. squarrosa* has been tested by a number of workers. The conclusions, however, were not consistent. Experiment of MAAN *et al.* (1981) using F_8 lines came to a rather negative conclusion that no appreciably high-yielding lines could be derived from the cross combination carrying *squarrosa* cytoplasm. KONZAK and ALLAN (1984) on the other hand have suggested that some promising lines could be segregated in the cross combinations carrying *squarrosa* cytoplasm. Desirable effect

of *squarrosa* cytoplasm was not unambiguously recognized in the present experiment; statistically significant increase of genetic variation was not found, and rather, a reduced variation was perceived for heading date and ear length. Effect of *longissima* cytoplasm also was not so much eminent and consistent as that of *kotschyi* cytoplasm.

Some correspondence could be recognized between the results of this experiment and the genetic relatedness among cytoplasms. According to the genetic distance which was calculated based on the modification spectrum of morpho-physiological characters of wheats by alien cytoplasms (TSUNEWAKI 1980), cytoplasm of *Ae. kotschyi* was shown to be considerably far deviated from those of *Ae. squarrosa*, *Ae. speltoides*, *Ae. longissima* and wheat (*T. aestivum*). The latter three *Aegilops* cytoplasms appeared rather closely related each other and not much deviated from wheat cytoplasm, while *Ae. speltoides* showed some distance from the other two *Aegilops* species. This phylogenetic relation among the *Aegilops* cytoplasms seems to have well been reflected in the amount of genetic variability of the alloplasmic crosses. Cytoplasm of *Ae. kotschyi* produced the most prominent effects. It increased the genetic variability of the seven out of ten characters measured, releasing the richest variety of transgressive lines. Cytoplasm of *Ae. speltoides* showed the second most noticeable effect, widening the range of the four out of ten characters. The results of *squarrosa* and *longissima* cytoplasms were not encouraging. A suggestion then may be drawn that new and desirable nucleo-cytoplasmic interactions are likely to occur when cytoplasmic and nuclear genomes are related with a moderate distance.

It has been revealed that plasma genes of *Aegilops* and *Triticum* species are genetically very stable and transmitted only through female gametes, and that there is no genetic differentiation in the cytoplasms of common wheats (TSUNEWAKI and TSUJIMOTO 1984). Then, if nuclear genes of the *Aegilops* species and/or Chinese Spring in the nuclear genomes of the alloplasmic parental lines have been completely replaced by those of Norin 26, there should be no differences among the cross combinations with eucytoplasm.

Differences among euplasmic crosses were frequently observed in the present experiment, though not statistically significant in most cases. Both of reciprocals in some cross combinations exhibited similar deviations from the check crosses of euplasmic Norin 26 and Norin 61. It is then estimated that some residual nuclear genes of the *Aegilops* species and/or Chinese Spring remained unsubstituted in the alloplasmic parental lines used in the present experiment. Segregation of residual alien genes has often been reported in this type of experiments using alloplasmic lines. Preferential transmission of particular genes and chromosomes has been suggested as a possible mechanism of residual genes being maintained after a number of repeated backcrosses (KOFOLD and MAAN 1980, TSUJI 1980).

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異種細胞質利用によるパンコムギの遺伝的変異の拡大——農林 26 号×農林 61 号
の F₃ 世代の遺伝的変異に対するエギロプス属 4 種細胞質の効果

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異種細胞質および正常細胞質をもつ農林 26 号と正常細胞質をもつ農林 61 号との正逆交配に由来する計 460 の F₃ 系統を用い, エギロプス属種, すなわち *Aegilops squarrosa*, *Ae. kotschy*, *Ae. speltoides*, および *Ae. longissima* の細胞質がパンコムギの農業形質の遺伝的変異にどのような効果を及ぼすかをみた。これら 4 異種細胞質のうち, 前 2 者については正逆交配こみで各 100 F₃ 系統を, 対照交配すなわち正常細胞質をもつ農林 26 号と農林 61 号の正逆交配に由来する 100 F₃ 系統とともに, 1982 年に 2 回反復の分割区法 (15 個体/反復区/系統) で圃場に栽植して形質調査を行なった。また, 後 2 者については正逆交配こみで各 60 系統を, 対照交配由来の 40 系統とともに, 1983 年に前年と同様に栽植して形質調査を行なった。調査形質は, 出穂日, 止葉長, 穂長, 穂重, 穂数/個体, 穂長, 第 1~3 節間長の 9 形質に, 草型の指標形質として計算した第 1 節間長と稈長の比を加えた計 10 形質である。

既報 F₂ での結果 (TSUNEWAKI *et al.* 1985) と同様, 本実験 F₃ においても, *Ae. kotschy* の細胞質が最も顕著な効果を示し, 調査 10 形質中 7 形質, すなわち出穂日, 穂長, 穂重, 稈長, 第 1~3 節間長の遺伝分散が

るいは遺伝率を増加させた。 *Ae. kotschy* 細胞質をもつ変異系統の中には、葉や穂の大きさのように収量性に関与する形質が正常細胞質系統と変らず、出穂日だけが有意に早生化したものが含まれていた。次に著しい効果を示したのは、*Ae. speltooides* の細胞質で、稈長、穂長、節間長など長さに関係する形質の遺伝分散を拡大した。*Ae. squarrosa* と *Ae. longissima* の細胞質の効果は、いずれの形質についてもあまり明瞭ではなく、形質によっては変異が減少する場合が認められた。2形質間の相関係数および調査全形質に対する主成分分析により、形質間の相関に対する上記異種細胞質の影響をみた結果、これらの異種細胞質は、個々の形質の変異幅あるいは変異域を変化させることはあっても、形質間の関係すなわち形質変異の相にはほとんど影響を与えないことが認められた。また本実験の結果と、従来の実験から推定された細胞質間の遺伝的近縁度(TSUNEWAKI 1980)との対比から、育種的に有望な核細胞質組合せが生じる可能性は、系統進化上近い関係にある核ゲノムと細胞質の組合せよりも、比較的遠縁のものとの間の組合せの方が大きいことが示された。