The Cytogenetics of Intergeneric Hybrids of Crossing *Triticum durum* and *Triticum timopheevi* with Tetraploid *Elytrigia elongata*

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ABSTRACT

In two crossing combinations, Triticum timopheevi X Elytrigia elongata(4x) and Triticum durum X Elytrigia elongata(4x), the hybrids were obtained at 0.4879 and 1.43 percent of pollinated florets, and the chromosome configurations at first meiotic metaphase in F_1 plants were 9.10'+9.11"+0.20"' and 13.78'+6.87"+0.147"', respectively. Chromosome association was likely due to autosyndesis between E_1 and E_2 genomes of E. elongata(4x) and homoeologous pairing between A and G genomes of T. timopheevi. It was concluded that bivalentization mechanism in T. timopheevi may have not been perfect, or the gene(s) of promoting pairing from E. elongata may be excessively expressed in the background such as AGE_1E_2 genome constitution.

Key words: intergeneric hybrids; homoeologous pairing; bivalentization; Triticum timopheevi; Triticum durum; Elytrigia elongata(4x).

INTRODUCTION

Elytrigia elongata(=Agropyron elongatum) is a polyploid complex represented by diploid(2n=2x=14), tetraploid(2n=4x=28), and decaploid(2n=10x=70) cytotypes. The tetraploid cytotype has been considered an autoploid, having a diploid-like cytological behaviour at first meiotic metaphase, owing to special diploidization mechanism(Heneen and Runemark 1972; Dvorak 1981b; Charpentier et al. 1986, 1988a). It was believed that slight differentiation occured between two genomes in tetraploid E. elongata, and this was supported by degree and pattern of chromosome pairing in F_1 triploid hybrids between diploid and tetraploid cytotypes(Dvorak 1981b; Charpentier et al. 1986) and between tetraploid E. elongata and common wheat(Charpentier et al. 1988a).

Dvorak(1987) allocated genes that promote and suppress homoeologous pairing in diploid E. elongata, and it appeared that the homoeologous promoters were associated with 3E and 5E chromosomes (Charpentier et al. 1988b). Charpentier et al.(1988b) believed that natural tetraploid E. elongata has lost the ability to induce homoeologous pairing. The evolution of bivalent pairing in the tetraploid form was related to the inactivation of the pairing-promoting system of the diploid form(Dvorak 1981a).

Hybridization between tetraploid E. elongata and common wheat was reported(Dvorak 1981b; Sharma and Gill 1983), and the hybrids showed a relatively high level of chromosome pairing at first mei-

otic metaphase,which can be interpreted as autosyndetic pairing of Elytrigia E_1 and E_2 chromosomes, and it further confirmed the homologous between E_1 and E_2 genomes and hence the autoploid nature of the tetraploid(Charpentier et al. 1988a).

In this work, tetraploid Elytrigia elongata was crossed with two species of tetraploid wheat, Triticum durum and T. timopheevi, in order to investigate the possibility of the crosses, and to examine the difference of chromosome pairing between different crossing combinations. We used the conventional methods of crossing to first obtain the two hybrids. And the homoeologous relationships of different genomes involved in these crossing combinations are discussed.

MATERIALS AND METHODS

Elytrigia elongata (Host.) Nevski (4x): Seeds were obtained from material produced at Northwest Institute of Botany, Xi'an, China(originally from D.R. Dewey, Crops Research Laboratory, Utah State University).

Triticum timopheevi Zhuk. and T. durum Desf. cv. "Italy 363": Seeds were obtained from Heilongjiang Academy of Agricultural Sciences, Harbin, China.

Producing hybrids: Two cross combinations, T. timopheevi X E. elongata(4x) and T. durum cv "Italy 363" X E. elongata(4x), were performed in the greenhouse as well as in the field, however, the

field crosses were not successful. Seeds of E. elongata(4x) were planted in the greenhouse in 1984, and later, the plants appeared as perennial, and they were crossed with T. timopheevi in June, 1986. Six grains of hybrid seeds were obtained from which two seedlings survived. Seeds of T. durum cv. "Italy 363" were planted in pots at the begining of spring, 1987, and were pollinated with perennial plants of tetraploid E. elongata outside the greenhouse in early June of the year. Eleven grains of hybrid seeds were obtained from which three seedlings survived(Table 1).

For purpose of observing meiosis in pollen mother cells, spikes were fixed in Carnoy(absolute alcohol, chloroform and acetic acid, 6:3:1) and stained according to iron-hematoxylin method. Anthers were squashed in 45% acetic acid, and microphotographed with Olympus BH-2 microscope.

RESULTS

The rate of recovery of seedlings was 0.478% in cross combination of T. timopheevi X E. elongata(4x)and 1.43% of T. durum X E. elongata(4x), respectively. The difference was significant. With T. durum cv. "Italy 363" as maternal parent, the number of hybrid seeds produced from the crossed generation was more than that of cross combination with T. timopheevi as maternal parent, but the proportion of well-differentiated embryos was less(Table 1).

Both hybrids were similar to their paternal parent, tetraploid E. elongata, morphologically and were perennial and self-sterile

biologically, and were likely resistant to rust and powdery mildew(Fig. 1).

Chromosome behaviour during meiosis of pollen mother cells of F_1 and their parents was observed. Chromosome pairing in hybrids is shown in Table 2. In F_1 with T. timopheevi as maternal parent, all of the pollen mother cells observed possessed at least three bivalents and an average of 9.11 bivalents, while an average of 6.87 bivalents was observed in F_1 with T. durum as maternal parent. A large number of lagging chromosomes in Anaphase I and micronuclei in all of tetracytes occurred in both hybrid combinations. In contrast with the hybrid, regular bivalents and occasional quatrivalents were arranged on equatorial plate of PMCs of tetraploid E. elongata(Fig. I, II).

DISCUSSION

Jenkins and Mochizuk (1957) obtained an amphiploid by a cross Triticum durum with diploid Agropyron(=Elytrigia) elongatum. Hybridization between tetraploid E. elongata and common wheat has been reported (Dvorak 1981b; Sharma and Gill 1983). Crossing Triticum timopheevi with decaploid E. elongata was made by Mujeeb-Kazi and Rodriguez (1981). The work of crossing T. durum and T. timopheevi with E. elongata by preceding investigators (see Knobloch 1968) appears to seldom involve the tetraploid E. elongata. This experiment, however, shows positive results of hybrids arising from the crossing of T. durum and T. timopheevi with tetra-

ploid E. elongata.

In tetraploid E. elongata, the diploidization is controlled by a special system of genes according to karyotypic analysis and analysis concerning morphology and geographic distribution of diploid and tetraploid elongata (Heneen and Runemark 1972). An antimorph of the pairing-promoting allele suppresses homoeologous pairing and induces bivalent pairing, and this antimorph is recessive to the promoters (Charpentier et al. 1986). Similar situations were also reported in Triticum longissim um (Avivi 1976) and in Avena strigosa (Ladizinsky 1973). It is believed that the E_1 and E_2 genomes in tetraploid E. elongata all originated from the E genome of diploid cytotype. Configurations of chromosome pairing at first meiotic metaphase in hybrids between diploid and tetraploid E. elongata were 2.2"' + 5.6" (Dvorak 1981b), or 2.83"' + 4.5" (Charpentier et al. 1986). The bivalents present in hybrids between common wheat and tetraploid E. elongata should be regarded as autosyndetic pairing between distant homologous of genomes E_1 and E_2 of E. elongata (Charpentier et al. 1988b). On the basis of the above metioned, chromosome pairing in hybrids between tetraploid wheat and tetraploid E. elongata should be also induced by the autosyndesis between homoeologous of genomes E_1 and E_2 of E. elongata.

Our data indicate that the average number of 6.87 bivalents at first meiotic metaphase in hybrids between T. durum cv. "Ita-

ly 363" and tetraploid E. elongata is in accord with the observations in hybrids between common wheat and tetraploid E. elongata (Dvorak 1981b; Sharma and Gill 1983; Charpentier et al. 1988a). However, it is noticeable that the average number of 9.11 bivalents, even so much as 13 bivalents, were observed in hybrids between T. timopheevi and tetraploid E. elongata. Since the hybrids are amphihaploid , it is necessary to compare the chromosome association in the hybrids with that of their parents being in haploid and diploid forms. Table 3 shows that more than 7 bivalents in the hybrids contrast with less than 0.3 bivalents in haploid form of T. timopheevi. Since 7 bivalents are possible homoeologous pairing between E_1 and E_2 of E. elongata, it should be reasonable to expect that autosyndetic pairing occurred between A and G genomes of T. timopheevi. In addition, at least 6 bivalents were observed in hybrids with T. timopheevi, indicating a great stability of the meiosis than combination with T. durum (Table 2).

Although Kerby and Kuspira (1988) provided new cytological evidence supporting the origin of B genome in polyploid wheat, and Tsunewaki (see his review 1989) proposed phylogenetic relationships between all Triticum and Aegilops species according to their plasmon as well as nuclear genome relationships, the origin of B and G genomes has still been the subject of considerable speculation and investigation, and still remains largely unsolved

(Miller 1987). Wagenaar (1961) observed the average numbers of chromosome association in the hybrids between T. timopheevi and T. durum as being 6.66 univalents, 9.04 bivalents, 1.06 trivalents and 0.03 quatrivalents. He showed later that the bivalent number was 13.9 in hybrids between T. timopheevi and T. dicoccoides(Wagenaar 1966). Feldman (1966) convincingly showed that most of the pairing failure in common wheat-timopheevi hybrids involved chromosomes of aestivum B and the corresponding genome of T. timopheevi, due to chromosome structural differences rather than genes causing asynapsis, and pointed out that no evidence was available suggesting that T. timopheevii actually evolved from T. turgidum, or the other way around. Hutchinson and Miller (1982) compared chromosomes of T. timopheevi with related wheats using C-banding and in situ hybridization techniques, and pointed out that there were marked differences in the distribution of heterochromatin between B and G genomes, and suggested the heterochromatin caused the reduced chiasma frequency, and that, in addition, T. timopheevi and T. dicoccum chromosome translocations exist within A genome and between the A and B or G genomes.

Data from present investigation further confirm the homology between E_1 and E_2 genomes, and suggest that bivalentization gene system of T. timopheevi is different from that of T durum: the effect of chromosome pairing in timopheevi-elongata hybrids is similar to that in tetraploid E. elongata X common wheat difi-

cient for Ph1, whreas that in durum-elongata hybrids is the same as the crossing in the presence of one dose of Ph1 (Charpentier et al. 1988a), indicating that dominant bivalentization gene such as Ph1 does not exist in T. timopheevi or, on the other hand, the gene(s) promoting homoeologous pairing of E_1 and/or E_2 may be expressed as relatively active background of AGE_1E_2 genome constitution as noting the effect of chromosome association in haploid T. timopheevi (Table 3). According to Zohary and Feldman (1962), in T. durum and T. timopheevi there are more differences between the differential genomes B and G than that between common (pivotal) genomes A. Wagenaar's investigations (1961, 1966) showed that T. timopheevi appears evolutionally to have a greater degree of relationship to T. dicoccoides than to T. durum. The bivalentization gene system of T. timopheevi may not be very perfect so that it must be complemented by additional mechanism (e.g. cytoplasmic male sterility) to keep the stability of the species.

Chromosome pairing, then, must be the basis for establishing chromosome recombination, and thus make breeding possible.

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Table 1. Frequency of hybrid F_1 seedlings obtained.

Hybrid combination	Floret No. pollenated	Seed No. obtained	Well-differentiated embryo No.	Seedlings obtained(%)
T. timopheevi X *E. elongata* 4x	426	6	5	2 (0.4785)
T. durum cv. "Italy 363" X *E. elongata* 4x	208	11	7	3 (1.4300)

Table 2. Chromosome association at first meiotic metaphase in F_1 and in E.elongata 4x

Combination or material	Chromosome No. (Genome formula)	Cell No.	I	II			III
				rod	ring	total	
T. timopheevi X E. elongata 4x	28 (AGE_1E_2)	139	9.10±0.25 (2-16)	4.51±0.13 (1-7)	4.56±0.13 (1-7)	9.11±0.12 (6-13)	0.20±0.12 (0-3)
T. durum X E. elongata 4x	28 (ABE_1E_2)	61	13.78±0.28 (10-28)	3.82±0.21 (0-6)	3.05±0.20 (0-7)	6.87±0.14 (0-9)	0.15±0.05 (0-1)
E. elongata 4x	28 ($E_1E_1E_2E_2$)		0.15			13.74	0.077

Table 3. Configurations of chromosome association at first meiotic metaphase in amphihaploid F_1 and their parents being in haploid and diploid forms.

Material	Meiotic configuration	Reference
T. timopheevi(2n)	0.64' + 13.96" + 0.005"'	Zhang *et al.* 1985
T. timopheevi(1n)	13.14' + 0.28" + 0.015"'	Simonet 1954*, Riley and Chapman 1957
F_1(*T.timopheevi* X *E.elongata* 4x)	9.10' + 9.11" + 0.20"'	
T. durum(2n)	1.005' + 13.97"	Zhang *et al.* 1985
T. durum(1n)	13.48' + 0.24"	Kihara 1926; Lacadena 1968; Kimber 1978
F_1(*T.durum* X *E.elongata* 4x)	13.79' + 6.87" + 0.15"'	
E. elongata 4x	0.15' + 13.74" + 0.077"'	

* Datum from Lacadena 1968.

Fig.I: Spike morphology of (from left to right) *T. durum* cv. "Italy 363", *T. timopheevi* , F_1(*T. timopheevi* X *E. elongata* 4x) (double), *E. elongata* 4x (single).

Fig. II: Chromosome pairing at first meiotic metaphase in hybrids and in *E. elongata* 4x. 1, *E. elongata* 4x, 14"; 2, *E. elongata* 4x, 12" + 1""; 3, 4 and 5, F_1(*T. timopheevi* X *E. elongata* 4x), 9" + 10', 9" + 10', 12" + 4'; 6, 7 and 8, F_1(*T. durum* X *E. elongata* 4x), 11" + 6', 9" + 10', and 8" + 1"' + 9'.

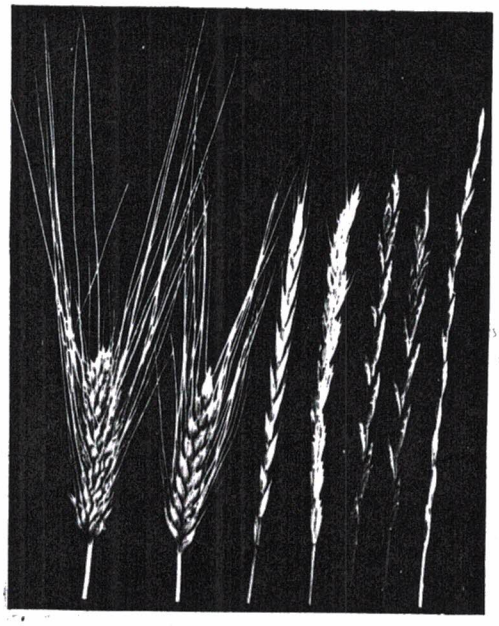

Fig. I

Fig II