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CYTOGENETIC STUDIES IN *TRITICUM-ELYTRIGIA* AMPHIPLOID HYBRIDS

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SUMMARY

Meiotic and fertility studies in two *T. durum/E. disticha* amphiploids (2n=56) and their BC_1F_1 progeny (2n=42) verified that the two genomes of *E. disticha* (2n=4x=28) differ from those of wheat, but resemble each other. Eight *T. durum/E. disticha* amphiploid//*T. durum* back-cross hybrids (2n=42), when crossed with eight *T. durum* (or *T. turgidum*)/*E. elongata* amphiploids (2n=42) gave a good kernel set. The 41.8% F_1 plants with 2n=42 had a mean of 16.94 bivalents and 0.6 multivalents/PMC, and produced 31.8 kernels/spike. The two genomes of *E. disticha* evidently resemble the E-genome of *E. elongata* and should be designated E^d_1 and E^d_2. *E. disticha* is therefore a segmental allotetraploid with the genomic constitution $E^d_1E^d_1E^d_2E^d_2$.

INTRODUCTION

Successful crosses between *Elytrigia disticha* (Thunb.) Prokudin ex Love (=*Agropyron distichum* (Thunb.) Beauv.), an indigenous littoral perennial with 2n=28, and the hexaploid wheat cultivars "Chinese Spring" and "Inia 66", as well as the durum cultivars "Calvin" and "Nordum", have made it possible to study the genomic relationships of these species (see Pienaar 1981). The cytogenetic investigations of Pienaar (1981) indicated that *E. disticha* is a segmental allotetraploid with genomes unlike those of wheat.

The present study was undertaken to clarify the polyploid nature of *E. disticha* and to determine the relationship of its genomes, tentatively designated X_1 and X_2, with the E-genome of diploid *E. elongata* (Host) Holub (=*Agropyron elongatum* (Host) B.P.).

MATERIALS AND METHODS

The *T. durum/E. disticha* F_1 hybrids referred to above were amphiploidised using the colchicine technique described by Pienaar (1981). The fertile C_1 sectors and the C_2 progeny with 2n=56, were back-crossed to *E. disticha*, to both durum parents, and to 20 other durum cultivars and experimental lines. Meiotic investigations were made on the progeny which had 42 chromosomes. The latter BC_1F_1 plants from eight lines were crossed with eight *T. durum* (or *T. turgidum*)/*E. elongata* amphiploids (2n=42), kindly supplied by Dr. B. C. Jenkins, Salinas, California, U.S.A., and Dr. L. H. Shebeski, University of Manitoba, Winnipeg, Canada. The F_1 progeny of these crosses having 2n=42 were used for the meiotic investigations.

Dr. G. Kimber, Columbia, Mo, U.S.A., analysed the relative affinities of the genomes

Table 1. Fertility of *Triticum-E. disticha* hybrids and derivatives, and the chromosome numbers of the progeny.

Pedigree of cross, amphiploid, back-cross and derivatives	No. kernels/ spike (% kernel set)	% Germi- nation	Seedling generation (total karyotyped), and % with 2n of:															
					<50	50	51	52	53	54	55	56	57	58	59	60	>60
2 *T. durum* cvs./*E. disticha*, C_1	2.5(2.1)	97.1	C_2	(67)	1.5		1.5	4.5	4.5	16.4	29.8	37.3	4.5				
2 *T. durum* cvs./*E. disticha*, C_2	8.1(10.4)	87.5	C_3	(35)				5.7	14.3	2.9	20.8	54.3	2.9				
2 *T. durum* cvs./*E. disticha*, C_3	11.3(13.5)	87.9	C_4	(66)				1.5	4.5	24.2	24.2	37.9	7.6				
2 *T. durum* cvs./*E. disticha*, C_4	15.0(15.6)	96.7	C_5	(111)			1.8	3.6	13.5	24.3	31.5	21.6	3.6				
				2n=	<36	36	37	38	39	40	41	42	43	44	45	46	>46
E. disticha × *T. durum* cv. "Nordum"/*E. disticha*	6.0(10.0)	16.8	BC_1F_1	(1)								100					
22 *T. durum* cvs. × 2 *T. durum* cvs./ *E. disticha*	17.1(67.8)	69.4	BC_1F_1	(351)			0.3		1.4	5.7	19.7	70.7	2.0		0.3		
20 *T. durum* cvs.//2 *T. durum* cvs./ *E. disticha*, BC_1F_1	15.6(22.4)	88.9	BC_1F_2	(241)		0.4		1.2	4.6	22.4	35.3	29.9	5.4	0.8			
10 *T. durum* cvs.//2 *T. durum* cvs./ *E. disticha*, BC_1F_2	22.8(36.3)	96.6	BC_1F_3	(170)				0.6	1.8	10.7	33.7	46.2	5.9	1.2			0.6
8 *T. durum* cvs.//2 *T. durum* cvs./ *E. disticha*, BC_1F_3	27.7(35.8)	96.7	BC_1F_4	(285)	0.4				1.4	4.9	27.0	62.1	4.2				
T. durum//*T. durum*/*E. disticha* × *T. durum* (or *turgidum*)/*E. elongata*, 22 crosses	13.3(39.8)	81.2	F_1	(158)	0.6				3.2	7.0	42.4	41.8	4.4				0.6
T. durum//*T. durum*/*E. disticha*/3/ *T. durum* (or *turgidum*)/*E. elongata*, F_1 of 17 crosses	31.8(34.6)	96.1	F_2	(216)	0.5	0.5	0.9	6.0	13.9	21.3	25.5	17.6	9.7	1.9	1.4	0.5	0.5
T. durum//*T. durum*/*E. disticha*/3/ *T. durum* (or *turgidum*)/*E. elongata*, F_2 of 9 crosses	31.3(36.4)	96.5	F_3	(220)			0.4	1.4	5.5	14.5	34.1	29.1	10.5	3.2	0.9	0.4	

				2n=	<62	62	63	64	65	66	67	68	69	70	71	72	>72
T. aestivum cv. "Inia 66"/ *E. disticha*, C_1	5.2(5.7)	92.3	C_2	(24)						4.2	29.2	41.7	20.8	4.2			
T. aestivum cv. "Inia 66"/ *E. disticha*, C_2	36.0(48.0)	95.0	C_3	(18)	16.7					5.6	16.7	44.4	16.7				
T. aestivum cv. "Inia 66"/ *E. disticha*, C_3	1.4(2.4)	94.7	C_4	(18)	5.6		5.6		5.6	11.1	16.7	38.9	5.6	5.6		5.6	
T. aestivum cv. "Inia 66"/ *E. disticha*, C_4	—	—	94.4	C_5	(34)	2.9	5.9	2.9		11.8	23.5	26.5	20.6	2.9		2.9		
T. aestivum cv. "Inia 66"/ *E. disticha*, C_5	11.8(16.3)	100.0	C_6	(18)				5.6		5.6	11.1	5.6	50.0	16.7	5.6		

				2n=	<50	50	51	52	53	54	55	56	57	58	59	60	>60
"Inia 66"/*E. disticha*×"Inia 66"	40.0(47.1)	95.0	BC_1F_1	(37)				8.1	13.5	27.0	35.1	16.2					
"Inia 66"/*E. disticha*//2 *T. aestivum* cvs., BC_1F_1	43.0(48.9)	100.0	BC_1F_2	(120)				2.5	10.0	17.5	29,2	27.5	8.3	4.2	0.8		
"Inia 66"/*E. disticha*//2 *T. aestivum* cvs., BC_1F_2	11.2(16.4)	98.0	BC_1F_3	(49)				2.0	12.2	24.5	18.4	26.5	14.3	2.0			
"Inia 66"/*E. disticha*//2 *T. aestivum* cvs., BC_1F_3	—	—	98.2	BC_1F_4	(109)			3.7	1.8	11.9	16.5	27.5	25.7	9.2	1.8	0.9		0.9
"Inia 66"/*E. disticha*//2 *T. aestivum* cvs., BC_1F_4	43.1(44.9)	99.4	BC_1F_5	(159)				0.6	1.9	8.2	29.6	52.8	4.4	2.5			

Table 2. Mean chromosome associations at first meiotic metaphase, and anaphase I segregation in PMC's of:
(a) *T. durum* cv. "Nordum"/*E. disticha*, F_1-hybrid (2n=28)
(b) *T. durum* (2 cultivars)/*E. disticha*, C_2 amphiploid (2n=56)
(c) *E. disticha*//*T. durum* cv. "Nordum"/*E. disticha* amphiploid, BC_1F_1 back-cross (2n=42)
(d) *T. durum* cv. "Calvin"//"Calvin"/*E. disticha* amphiploid, BC_1F_1 back-cross (2n=42)
(e) *T. durum* (or *T. turgidum*)/*E. elongata* amphiploids/3/*T. durum*//*T. durum*/*E. disticha* back-crosses, F_1 of 6 crosses (2n=42)
(f) *T. aestivum* cv. "Inia 66"/*E. disticha*, F_1-hybrid (2n=35)
(g) *T. aestivum* cv. "Inia 66"/*E. disticha*, C_1 amphiploid sectors (2n=70)
(h) *T. aestivum* cv. "Inia 66"/*E. disticha*//"Inia 66", BC_1F_1 back-cross (2n=56)

Cross and no. PMC's examined		2n	Genomes	Metaphase I chromosome associations								Chiasmata/PMC		No. of PMC's at AI	Anaphase I segregation P1–Lag.–P2
				Uni-valents	Bivalents			Multivalents							
					Rod	Ring	Total	III	IV (open)	IV (closed)	V+	Total	Terminal		
(a)	200	28	$ABE_1^dE_2^d$	14.12 (6-26)*	3.55 (0-7)	1.26 (0-4)	4.81 (1-9)	0.38 (0-2)	0.75 (0-2)		0.02 (0-1)	9.17 (1-14)	9.08 (1-14)	30	8.03-12.33-7.63 (6-11)-(7-16)-(6-10)
(b)	100	56	$AABBE_1^dE_1^d$–$E_2^dE_2^d$	2.61 (0-8)	5.65 (1-12)	18.58 (13-26)	24.23 (19-28)	0.63 (0-2)	0.47 (0-3)	0.24 (0-2)	0.04 (0-1)	50.55 (44-57)	43.26 (38-50)	60	27.7-1.8-26.6 (24-29)-(0-9)-(23-28)
(c)	100	42	$ABE_1^dE_1^dE_2^dE_2^d$	14.09 (11-18)	1.73 (0-5)	10.4 (5-14)	12.13 (8-15)	0.26 (0-2)	0.3 (0-2)	0.39 (0-3)	0.02 (0-1)	30.47 (26-35)	20.9 (16-25)	20	15.0-13.1-13.9 (13-18)-(10-16)-(13-15)
(d)	100	42	$AABBE_1^dE_2^d$	3.18 (0-8)	4.42 (1-10)	14.40 (10-18)	18.82 (16-21)	0.12 (0-1)	0.19 (0-1)	0	0	34.35 (28-39)	33.25 (27-37)	15	21.0-1.5-19.5 (20-22)-(0-13)-(19-21)
(e)	300	42	$AABBEE_{1-2}^d$	6.06 (0-22)	4.79 (0-12)	12.14 (5-18)	16.94 (10-21)	0.37 (0-3)	0.21 (0-2)	0.02 (0-1)	0.003 (0-1)	30.87 (18-48)	29.48 (16-39)	90	19.1-4.7-18.2 (15-24)-(0-12)-(14-21)
(f)	300	35	$ABDE_1^dE_2^d$	23.78 (15-35)	4.05 (0-9)	0.60 (0-4)	4.65 (0-10)	0.44 (0-2)	0.15 (0-1)		0 (0)	6.59 (0-12)	6.41 (0-12)	5	18.0-1.2-15.8 (15-21)-(1-5)-(14-17)
(g)	20	70	$AABBDD$–$E_1^dE_1^dE_2^dE_2^d$	6.1 (2-10)	—	—	29.58 (30-34)	0.63 (0-2)	0.71 (0-2)		—	—	—	25	35.0-0.8-34.2 (34-36)-(0-3)-(33-35)
(h)	100	56	$AABBDD$–$E_1^dE_2^d$	5.34 (2-10)	6.77 (1-13)	17.88 (11-22)	24.76 (18-27)	0.18 (0-2)	0.18 (0-2)		0 (0)	45.32 (37-51)	39.53 (27-49)	1	26-4-26

* Range in brackets

of the F_1-hybrids with numerical techniques developed in his laboratory (see Kimber 1982a).

RESULTS

After colchicine treatment the cloned *T. durum/E. disticha* F_1 plants produced fertile C_1 sectors which on selfing and back-crossing to *T. durum* and *E. disticha* gave rise to many perennial C_2 and BC_1F_1 progeny. The fertility and chromosome numbers are given in Table 1. The PMC meiotic data from the euploid *T. durum/E. disticha* C_2 amphiploids ($2n=56$) and their BC_1F_1 back-cross plants ($2n=42$) are given in Table 2. In the C_2 amphiploids 33% of the PMC's had 26 or more bivalents. Their fertility, however, was rather low (10.4%), but it improved to 15.6% in the C_4 generation.

The *E. disticha*//"Nordum"/*E. disticha* BC_1F_1 plant with $2n=42$ was completely sterile with a high frequency of univalents (14.09/PMC, Table 2). In 44% of the PMC's 13 to 15 bivalents were counted. The reciprocal back-crosses, *T. durum//T. durum/E. disticha* ($2n=42$), were relatively fertile (22.4%) due to a low univalent and multivalent frequency. In fact, 30% of the PMC's had 20 or 21 bivalents at MI. The fertility improved to 35.8% in the BC_1F_3 generation.

Eight *T. durum//T. durum/E. disticha* BC_1F_1 back-cross lines ($2n=42$) when reciprocally crossed with eight *T. durum* (or *T. turgidum*)/*E. elongata* amphiploids ($2n=42$) gave a good kernel set of 39.8% (Table 1). The germination percentage was 81.2, and the 44% hybrid seedlings with $2n=42$, developed into vigorous plants. The mean meiotic associations of six of the hybrids are given in Table 2. Altogether 39.7% PMC's had 18 or more bivalents at MI. These hybrids had a higher fertility (34.2%) than the *T. durum//T. durum/E. disticha* BC_1F_1 plants. The fertility improved slightly to 36.4% in the euploid F_2 plants.

For comparative purposes the data of the *T. aestivum* cv. "Inia 66"/*E. disticha* hybrid, amphiploids and back-crosses described by Pienaar (1981) are included in Tables 1 and 2. It is evident that little progress was made in selecting for fertility in the amphiploids. Better results were obtained in the back-cross generations where the average fertility of the BC_1F_4 plants was 44.9%.

DISCUSSION

The meiotic studies in the *T. durum/E. disticha* and *T. aestivum/E. disticha* F_1 hybrids revealed synaptic associations between two closely related genomes. Pienaar (1981) interpreted this to stem from segmental allotetraploidy in *E. disticha*. His hypothesis is supported by the numerical analysis of the F_1 meiotic data by Kimber (1982b). This analysis indicates that there are two similar genomes in *E. disticha* which are different from the wheat genomes. To aid the discussion the genomic constitution of *E. disticha* can tentatively be designated $X_1X_1X_2X_2$, and those of the two F_1 hybrids above, ABX_1X_2 and $ABDX_1X_2$ respectively.

The 8x and 10x C_2 amphiploids derived from the latter two F_1 hybrids respectively had 1.15 and 1.34 multivalents/PMC. That these multivalents as well as the bivalents of the F_1 hybrids do in fact stem from associations between the X_1 and X_2 homoeologues can be deduced from the meiotic configurations in the back-cross hybrids.