Alien chromosome substitution of *durum* wheat: Substitution of the chromosome e_7 of *Elytrigia elongata* for chromosome 4A of Stewart *durum*¹⁾

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ABSTRACT

Four monosomic substitution lines of the *Elytrigia elongata* (= *Agropyron elongatum*) chromosomes, e_3 , e_5 , e_6 and e_7 for chromosome 4A of *durum* wheat were produced by the cross between monosomic 4A and the corresponding disomic addition lines of Stewart *durum*. Among them the monosomic substitution line $e_7(4A)$ was the most vigorous and fertile. Although this line showed a chromosome configuration of $13''+2'$ at the first meiotic metaphase, it had 14 bivalents at diakinesis in most of its pollen mother cells. The fertilization rate of the four types of the egg cells produced by this monosomic substitution suggested a 50% elimination of both e_7 and 4A univalents during the meiosis of *durum* wheat. Male transmission behavior indicated that chromosome e_7 compensates for the function of chromosome 4A in the certation. A disomic substitution line was selected from the progeny of the monosomic substitution line $e_7(4A)$. Plants of this line were vigorous and completely fertile. Chromosome e_7 was found to have a structural gene for alcohol dehydrogenase; in wheat this gene is known to be located on the three chromosomes of homoeologous group 4. It was thus concluded that chromosome e_7 of *E. elongata* belongs to homoeologous group 4. A comparison of the morphology of the substitution, addition and monosomic lines with those of the normal Stewart *durum*, showed that chromosome e_7 carried genes for awn suppression, culm thickness and ear laxness.

1. INTRODUCTION

Emmer wheats, including cultivated and wild species, have much genetic variation and are very useful as breeding materials of the cultivated emmer and common wheats. To promote the genetical analyses of the emmer wheats, Mochizuki (1968) produced a series of monosomics in an emmer wheat, *Triticum durum* cv. Stewart, by recurrent backcrosses of the 14 monosomics for the A and B genome-chromosomes of a common wheat, *T. aestivum* cv. Chinese Spring, to the recurrent parent Stewart *durum*. Most of the monosomics of

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Stewart *durum*, however, are not useful for genetic analyses because of reduced vigor, low fertility and low transmission rate. For the same purpose, Joppa and Williams (1977), Mochizuki and Nagayoshi (1977), Joppa *et al.* (1978) and Ono *et al.* (1980) produced some disomic substitution lines of *durum* wheat in which a pair of A or B genome-chromosomes was replaced by D genome-chromosomes of common wheat. Most of the substitution lines were more vigorous than the corresponding monosomics. Some of them, however, still showed low fertility, reduced vigor, or leaf color variegation (Joppa 1973, Mochizuki and Nagayoshi 1977). To overcome these deleterious effects which were assumed to have been caused by the deficiency of an A or B genome-chromosome, the homoeologous chromosome that well compensates for the function of the missing A or B genome-chromosome of *durum* wheat should be sought in other alien genomes. Mochizuki (1960, 1962) produced a series of disomic addition lines of Stewart *durum* with a pair of *Elytrigia elongata* (= *Agropyron elongatum*) chromosomes; each chromosome added was named e_1 to e_7 . Using these disomic addition lines and monosomics of Stewart *durum*, we produced a vigorous and fertile disomic substitution line, which is reported in this paper.

2. MATERIALS AND METHODS

The *E. elongata* disomic addition lines and the monosomic 4A of Stewart *durum* were used to produce the chromosome substitution lines. Monosomic 4A was crossed as the female to the six disomic addition lines e_1 to e_7 except e_4 , and two ditelocentric addition lines, e_4t^+ and e_4t^- ; these ditelocentric addition lines were used because disomic addition e_4 was very weak and could not be used as the pollen parent. In the F_1 generation, hybrids carrying 28 chromosomes which were expected to be the monosomic substitution type plants (chromosome number; $2n=28$, chromosome constitution; $AABB-4A+e_x$) were selected. They were self-pollinated to get disomic substitution lines ($2n=28$, $AABB-4A4A+e_xe_x$). Ditelocentric 4A α and 4BL of a common wheat, Chinese Spring, were crossed to the disomic substitution line for cytological confirmation of the deficiency of the chromosome 4A.

Usual acetocarmine squash and smear methods were used for the observation of mitotic chromosomes in the root tip cells and meiotic chromosome configuration in the pollen mother cells (PMCs), respectively.

Starch gel electrophoresis of the alcohol dehydrogenase (ADH: E.C. 1.1.1.1) of the disomic substitution line was performed by the continuous buffer system (Scandalios 1969), and its zymogram was compared with those of normal Stewart, disomic addition lines, amphiploid between Stewart and *E. elongata* and diploid *E. elongata*. Matured grains of these lines were soaked with distilled water for 24 hr at 25°C. One grain was ground with 0.3 ml

extraction buffer (Calson 1972), the homogenate was centrifuged for 20 minutes by $12000 \times g$, and the supernatant was used as the sample for electrophoresis. After electrophoresis for 18 hr at 140 V, the starch gel was stained by the mixture described by Hart (1970).

The following six quantitative characters of the substitution, addition and monosomic lines were compared with those of normal Stewart by t-test; plant height, tiller number, culm diameter at the position below 5cm from the neck of the spike, awn length from the tip of the apical floret, ear density and selfed seed fertility.

3. RESULTS

Production of the monosomic substitution lines for 4A

Table 1 shows the number of seeds obtained by the cross between monosomic 4A and disomic or ditelocentric addition lines. Five of the 53 F_1 's observed had 28 chromosomes which were expected to be monosomic substitution lines. One monosomic substitution plant $e_2(4A)$ was weak and died before heading. Plants of the substitution line $e_3(4A)$ and $e_6(4A)$ were relatively vigorous and showed $13'' + 2'$ at the first meiotic metaphase (MI). They were, however, almost completely sterile. On the other hand, the plants belonging to substitution line $e_7(4A)$ grew vigorously, were considerably fertile, and morphologically resembled normal Stewart *durum*.

Meiotic behavior of the two univalents in the monosomic substitution line

Table 2 shows the average chromosome configuration of this monosomic

Table 1. *Seed setting and somatic chromosome numbers of the progeny of the cross between monosomic 4A and disomic or ditelocentric addition lines of E. elongata*

F_1 line	No. florets crossed	No. seeds set	Chromosome no.		Selfed seed fertility of F_1 's with 28 chromosomes ¹⁾
			28	29	
Mono-4A $\times$ di-addition e_1	30	4	0	4	—
Mono-4A $\times$ di-addition e_2	62	11	1	8	(lethal)
Mono-4A $\times$ di-addition e_3	32	8	1	6	0.04
Mono-4A $\times$ ditelo-addition e_4t^1	30	6	0	6	—
Mono-4A $\times$ ditelo-addition e_4t^s	26	6	0	6	—
Mono-4A $\times$ di-addition e_5	30	7	0	7	—
Mono-4A $\times$ di-addition e_6	32	4	1	3	0.11
Mono-4A $\times$ di-addition e_7	26	10	2	8	1.10
Total	268	56	5	48	

1) Number of seeds per spikelet.

Table 2. *Average chromosome pairing at diakinesis (D) and the first meiotic metaphase (MI) of PMC's of the monosomic, addition, substitution and normal Stewart durum*

Line	Chromosome constitution	Somatic chromosome number	Stage	No. PMC's observed	Bivalent	Univalent
Monosomic 4A	AABB-4A	27	D MI	100 100	13.0 13.0	1.0 1.0
Nulli-monosomic addition e_7 (4A)	AABB-4A4A+ e_7	27	D MI	38 52	13.0 13.0	1.0 1.0
Stewart	AABB	28	D MI	100 100	14.0 14.0	0.0 0.0
Monosomic substitution e_7 (4A)	AABB-4A+ e_7	28	D MI	134 451	13.9 13.0	0.2 2.1
Disomic substitution e_7 (4A)	AABB-4A4A+ e_7	28	D MI	53 160	14.0 13.9	0.1 0.1
Monosomic addition e_7	AABB+ e_7	29	D MI	32 306	14.0 14.0	1.0 1.0
Disomic addition e_7	AABB+ e_7	30	MI	845	15.0	0.0

Fig. 1. Pollen mother cells of the monosomic substitution $e_7(4A)$ at diakinesis (A), late diakinesis, with a separating bivalent (arrowed) (B), the first metaphase (C), and the first anaphase (D); and those of monosomic addition line e_7 at diakinesis (E) and the first metaphase (F).

substitution $e_7(4A)$ line. Most of the PMCs showed $13''+2'$ at MI (Fig. 1C), but $14''$ at diakinesis (Fig. 1A). A dumb-bell shaped bivalent was found in many PMCs at late diakinesis (Fig. 1B). These findings indicate that the two univalents, $4A$ and e_7 , are precociously separated. At the first anaphase the two univalents split equationally in about two-thirds of PMCs (Fig. 1D). Consequently, most of the e_7-4A bivalents at diakinesis are divided into four chromosomes only in the first meiotic division.

Transmission of the chromosome e_7 through female and male gametes

The monosomic substitution line $e_7(4A)$ was crossed to normal Stewart

Table 3. Somatic chromosome numbers and the chromosome configuration at the first meiotic metaphase of the reciprocal F_1 's between Stewart and monosomic substitution line $e_7(4A)$, and the selfed progeny of monosomic substitution line $e_7(4A)$

Cross combination	Seed morphology	No. plants obtained	Chromosome no. and configuration				
			27	28	29	13''+1'	14''+1'
Monosomic substitution $e_7(4A)$ (φ) $\times$ Stewart	Shriveled	21	21 ²⁾	0	0	—	—
	Plump	14	0	3	9	—	2
	Total	35	21	3	9	—	2
	(%)	(100.0)	(60.0)	(8.6)	(25.7)	—	(5.7)
Stewart (φ) $\times$ monosomic substitution $e_7(4A)$	Shriveled	0	0	0	0	—	0
	Plump	49	0	30	19	—	0
	Total	49	0	30	19	—	0
	(%)	(100.0)	(0.0)	(61.2)	(38.8)	—	(0.0)
Monosomic substitution $e_7(4A)$ selfed	Shriveled	9	6	0	0	3	0
	Plump	18	2	4	9	2	1
	Total	27	8	4	9	5	1
	(%)	(100.0)	(29.6)	(14.8)	(33.3)	(18.5)	(3.7)

1) Nullisomic 4A monosomic addition e_7 type plant; chromosome constitution, $AABB-4A4A+e_7$.

2) This includes seven plants which died before chromosome counting.

durum reciprocally in order to estimate the transmission rate of chromosome e_7 through female and male gametes. Thirty-five seeds were obtained by the cross, $e_7(4A)$ (φ) $\times$ Stewart, in which 21 were shriveled (Table 3). All plants grown from the shriveled seeds had 27 chromosomes and showed $13''+1'$ at MI of PMCs. Of the 14 plants grown from the plump seeds, two had 29 chromosomes and the remainder had 28. No plants from the plump seeds were $2n=27$. The 28-chromosome plants were divided into two groups, one showing $14''$ and the other $13''+2'$. The observed ratio of the four plant types, $2n=27$: $2n=28$ ($14''$): $2n=28$ ($13''+2'$): $2n=29$, fitted the 9:3:3:1 ratio that is expected from 50% elimination of both univalents, e_7 and $4A$, during meiosis in the embryo sac mother cells, as is known to occur in common wheat (Sears 1944).

Monosomic substitution line $e_7(4A)$ crossed as male to normal Stewart *durum* produced 49 plump seeds but no shriveled seeds. All the plants raised from these seeds had 28 chromosomes, 30 of which showed the chromosome configuration $14''$ and 19 $13''+2'$ at MI of PMCs. This fact indicates that pollen grains carrying 13 or 15 chromosomes are inferior to those carrying 14 chromosomes in the certation, and that chromosome e_7 can compensate considerably for the function of chromosome $4A$ in the substitution-type male gametes.

Production of the disomic substitution line $e_7(4A)$

The plants belonging to the disomic substitution line $e_7(4A)$ were screened from the selfed progeny of the monosomic substitution line $e_7(4A)$ by observation of their chromosome number and meiotic configuration (Table 3). All nine plants from the shriveled seeds had 27 chromosomes, whereas the plump seeds produced three types of plants having the chromosome number of 27, 28 and 29. Four F_2 's showing $14''$ were identified as normal disomics, and a plant possessing 29 chromosomes was identified to be a monosomic addition line. Five plants possessing 27 chromosomes had shorter awns than the others, and were found to be nullisomic $4A$ monosomic addition e_7 type plants ($2n=27$, $AABB-4A4A+e_7$; Abbrev. nulli-monosomic addition line $e_7(4A)$) because the disomic F_1 between these short-awned plants and normal Stewart showed $13''+2'$ at MI of PMCs. From the selfed offspring of the nulli-monosomic addition line $e_7(4A)$, plants carrying 28 chromosomes which were expected to belong to the disomic substitution line $e_7(4A)$ were selected.

Ditelocentric $4A\alpha$ and $4BL$ of Chinese Spring were crossed to the disomic plants appearing among the selfed progeny of nulli-monosomic addition $e_7(4A)$ plants. No heteromorphic bivalents were formed in the PMCs of the F_1 's from the cross, disomic substitution $e_7(4A) \times$ ditelo- $4A\alpha$ (Fig. 2A). On the other hand, the F_1 's from the cross, disomic substitution $e_7(4A) \times$ ditelo- $4BL$ and normal Stewart $\times$ ditelo- $4A\alpha$ or $4BL$, formed a heteromorphic bivalent

Fig. 2. Pollen mother cells of the aneupentaploid F_1 's between disomic substitution $e_7(4A)$ of *durum* wheat and ditelocentric $4A\alpha$ and $4BL$ of a common wheat.

A: a PMC of the F_1 from the cross, disomic substitution $e_7(4A) \times$ ditelo- $4A\alpha$, showing $13''+9'$.

B: a PMC of the F_1 from the cross, disomic substitution $e_7(4A) \times$ ditelo- $4BL$, showing a heteromorphic bivalent (arrowed).

(Fig. 2B). This fact indicates that the chromosome $4A$ of Stewart *durum* was replaced by the e_7 of *E. elongata*.

Zymogram phenotype of ADH of the disomic substitution line $e_7(4A)$

Zymogram phenotypes of ADH of all the disomic addition lines of *E. elongata* except for the line e_7 were the same as that of Stewart *durum*. The disomic addition line e_7 and Stewart-*E. elongata* amphiploid, however, showed different zymogram phenotypes as shown in Fig. 3B and 3C, respectively. Their zymogram patterns were in good agreement with the model of Hart (1970), if the chromosome e_7 of *E. elongata* is assumed to produce an ADH

Fig. 3. Photograph of the ADH zymogram phenotypes.

- A: Stewart *durum*, AABB.
- B: Stewart-*E. elongata* amphiploid, AABBEE.
- C: disomic addition e_7 , AABB+ e_7e_7 .
- D: disomic substitution $e_7(4A)$, AABB-4A4A+ e_7e_7 .

protomer, ϵ , having the same electrophoretic mobility to the protomer β that was produced by chromosome 4B. Accordingly, the disomic substitution line $e_7(4A)$ as well as diploid *E. elongata* produced only one band (Fig. 3D) in which three equally charged dimers, $\beta\beta$, $\epsilon\epsilon$ and $\beta\epsilon$ of the former, and the $\epsilon\epsilon$ of the latter were located. This indicates that chromosome e_7 of *E. elongata* has a structural gene, *Adh_B*, for ADH.

Effects of chromosome e_7 and 4A on the quantitative characters of Stewart durum

Measurements of six quantitative characters of the Stewart *durum* and its substitution, addition and monosomic lines are given in Table 4. Disomic substitution plants had thicker and slightly shorter culms and laxer spikes with shorter awns than those of normal Stewart *durum*, but the number of tillers per plant and selfed seed fertility were not different from those of Stewart *durum*. Such differences between the disomic substitution and the normal Stewart *durum* were similar to those obtained by the nulli-monosomic addition $e_7(4A)$ and monosomic 4A. This indicated that chromosome e_7 of *E. elongata* has genes for suppressing plant height and awn length, and genes for culm thickness and ear laxness. The disomic addition line e_7 , however, had dense spikes, which suggests that the increase of dose of chromosome e_7 and 4A makes the spikes dense. The spikes of normal Stewart, and its substitution, addition and monosomic lines are shown in Fig. 4.

Table 4. *Quantitative characters of monosomic, substitution and addition lines, and their derivatives*

Line	Plant height (cm)	No. tillers	Culm diameter (mm)	Awn length (mm)	Ear density ¹⁾	Selfed seed fertility ²⁾
Stewart (1979)	167.0	10.8	2.30	139.6	21.9	2.25
Monosomic substitution e_7 (4A)	174.4	15.2**	2.51**	123.5**	20.6**	0.96**
Monosomic 4A	152.8**	9.5	1.72**	129.8**	23.3**	0.37**
Nulli-monosomic addition e_7 (4A)	145.0**	14.0	2.03	102.8**	18.9**	0.25**
Disomic addition e_7	123.0**	13.0	2.53**	94.5**	30.0**	0.23**
Stewart (1983)	153.3	9.0	1.62	137.0	27.8	1.92
Disomic substitution e_7 (4A)	146.9*	10.6	2.06**	78.0**	24.9**	1.95

* and **: Significant at the 5 and 1% level, respectively.

1) Number of spikelets per 10 cm rachis.

2) Number of seeds per spikelet.

Fig. 4. Spikes of normal Stewart durum (A), monosomic substitution e_7 (4A) (B), disomic substitution e_7 (4A) (C), disomic addition e_7 (D) and monosomic 4A (E).

4. DISCUSSION

In both the plant and pollen of the substitution line $e_7(4A)$, chromosome e_7 of *E. elongata* fully compensates for the functions of chromosome 4A of *durum* wheat. Furthermore, an electrophoretic study proved that chromosome e_7 had a structural gene for alcohol dehydrogenase that is known to be located on each group 4 homoeologue of common wheat (Hart 1970). These facts strongly suggest that chromosome e_7 of *E. elongata* is a homoeologue of the group 4 chromosomes, 4A, 4B and 4D of wheat. Consequently, chromosome e_7 should be named 4E.

Dvořák (1980) produced chromosome substitution lines of 4E of *E. elongata* for 4A, 4B and 4D of a common wheat, Chinese Spring. He reported that the disomic substitution line 4E(4A) was vigorous but almost sterile because genes on chromosome 4A which are indispensable for normal fertility were absent, and because chromosome 4E did not carry their homoeoalleles. By contrast, the disomic substitution line $e_7(4A)$ of Stewart *durum* was fully fertile (Table 4). The different fertility expression between the two disomic substitution lines is attributable to either the difference between two *E. elongata* chromosomes, 4E and e_7 , or that between chromosome 4A of Chinese Spring and Stewart *durum*. Hart and Tuleen (1983) reported that the 4E chromosome added to Chinese Spring genomes has a structural gene of ADH. The ADH gene on chromosome 4E codes for the protomer having a different electrophoretic mobility from those coded by wheat ADH genes, whereas the protomer coded by the present e_7 chromosome has the same mobility as that coded by a gene on chromosome 4B. These facts indicate that chromosome e_7 added to Stewart *durum* is not identical with chromosome 4E added to Chinese Spring.

The disomic addition line e_7 of Stewart *durum* had thick, stiff straw with erect leaves, dense spikes with short awns and low fertility (Table 4). These characteristics are common to those of the chromosome 4E addition line of Chinese Spring (Dvořák and Knott 1974; Dvořák and Sosulski 1974), although their deviation from the normal line (Stewart or Chinese Spring) was greater in the Stewart than in the Chinese Spring addition line. Also in the disomic substitution line $e_7(4A)$, some of these characters are affected by chromosome e_7 , whereas in the disomic substitution line 4E(4D) of Dvořák and Sosulski (1974) which resembles normal Chinese Spring, they are not. This fact suggests that the effects of an alien chromosome appear more drastically in the morphological characters of the tetraploid than the hexaploid wheats.

The association of chromosome e_7 and 4A at diakinesis may not be caused by a translocation between the two chromosomes because no trivalent is formed at either diakinesis or the MI of the PMCs of monosomic addition line e_7 (Table 2, Fig. 1E and 1F). This fact may suggest that chromosome e_7 of

E. elongata is partly homologous to chromosome 4A of *Stewart durum* to such an extent that they can pair weakly at the prophase of monosomic substitution, but not so firmly as to hold bivalency until the first metaphase. No recombination seems to occur between chromosome e_7 and 4A because the disomics, monosomics and monosomic substitution plants derived from the monosomic substitution plants were morphologically uniform in each of them.

Scoles and Kibirge-Sebunya (1983) reported the preferential transmission of an *E. elongata* chromosome $7el_2$ through female gametes. They pointed out that this chromosome was homoeologous to our chromosome e_7 . In the present investigation, however, chromosome e_7 was found to belong to homoeologous group 4, whereas chromosome $7el_2$ was reported to belong to homoeologous group 7 (Scoles and Kibirge-Sebunya 1983).

The present disomic substitution line $e_7(4A)$ is useful for the genetic analyses of emmer wheat because it is vigorous and completely fertile. In order to produce such vigorous and fertile alien chromosome substitution lines for other emmer wheat chromosomes, it is necessary to seek alien chromosomes which can compensate well for the function of the A and B-genome chromosomes in various relatives of wheat, such as *Aegilops*, *Secale*, *Haynaldia* and *Elytrigia* species.

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