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Cytogenetics of ditelotetrasomics for short arms of four chromosomes of barley (*Hordeum vulgare* L.)

T. Tsuchiya and S. Wang

Department of Agronomy, Colorado State University, Fort Collins, CO, USA

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Summary. Plants with a pair of extra homologous telocentric chromosomes in addition to the normal chromosome complement are called ditelotetrasomics. Six types of ditelotetrasomics of barley have been obtained. Four types obtained in the selfed progenies of telotrisomics (Triplo 2S, Triplo 5S, Triplo 6S, and Triplo 7S) are reported in this paper. The ditelotetra 2S showed a stronger expression of the diagnostic characteristics of Triplo 2S. It was weak and small, with narrow, short, dark-green leaves, and was almost completely pollen and seed sterile. However, three other ditelotetrasomics (ditelotetra 5S, 6S, and 7S) did not show specific diagnostic characteristics and were similar to normal diploid plants, with the exception of ditelotetrasomic 5S, which showed some effects. At meiotic diakinesis and metaphase I, these ditelotetrasomic plants showed chromosome configurations of $6_{II}+1_{IV}$, $7_{II}+1\,telo_{II}$, $6_{II}+1_{III}+1\,telo_{I}$, or $7_{II}+2\,telo_{I}$. Most of the sporocytes at anaphase and telophase in the first and second meiotic divisions showed almost normal chromosome behavior. Quartets were mostly normal with no micronuclei. Approximately 30% of the selfed progenies of these three ditelotetrasomics were ditelotetrasomics and almost 50% were telotrisomics, indicating a high percentage of male and female transmission of the extra telocentric chromosomes.

Key words: Barley – Chromosome arm – Telotrisomic – Ditelotetrasomic – Telocentric chromosome

Introduction

Telocentric chromosomes have been reported in several plant species, such as maize (Rhoades 1940), diploid wheat (Smith 1947; Moseman and Smith 1954), hexaploid wheat (Sears 1966; Sears and Sears 1978), and tomato (Khush and Rick 1968). The telotrisomics have been employed to associate genes with respective chromosome arms, to determine the centromere position on linkage maps, and to find the crossover distance between the marker and the centromere (Sears 1966; Khush and Rick 1968; Tsuchiya and Singh 1982; Tsuchiya 1983). In barley, telotrisomics have contributed greatly to genetic linkage mapping and cytogenetic studies (Tsuchiya 1991).

A ditelotetrasomic of barley was first found by Tsuchiya (1969), and was studied in detail by Fedak and Helgason (1970). Later, additional ditelotetrasomics were found (Singh and Tsuchiya 1977; Furuta and Tsuchiya 1987; Wang and Tsuchiya 1989). High transmission rates of extra telocentrics have been reported in selfed progenies of ditelotetrasomics (Fedak and Helgason 1970; Wang and Tsuchiya 1989). In addition, ditelotetrasomics have proved useful in further understanding the genetic architecture of barley chromosomes.

Several types of ditelotetrasomics have been found in barley; most viable ditelotetrasomics are those for the short arms of chromosomes (Table 1). However, only ditelotetrasomic 1S has been studied previously in detail (Fedak and Helgason 1970). This paper presents the cytogenetic studies of four ditelotetrasomics for the short arms of chromosomes 2, 5, 6, and 7.

Materials and methods

Four types of ditelotetrasomics of barley (for 2S, 5S, 6S, and 7S) have been obtained in the selfed progenies of telotrisomics (Table 1). The ditelotetrasomics, their related telotrisomics, and the diploid sibs were grown in the greenhouse. Morphological features, pollen fertility, and seed set were studied to compare ditelotetrasomics with their related telotrisomics and diploid sibs.

Table 1. The frequency of ditelotetrasomics and other cytotypes in the selfed progenies of telotrisomics of barley (numbers in parentheses are percentages)

Parental telotrisomics	Chromosome number					Total no. of plants
	14	14+1telo	14+2telos	15	Other	
1S	242 (56.8)	164 (38.4)	3 (0.7)	15 (3.6)	2 (0.5)	426[a]
	–	–	5 (1.0)	–	–	495[b]
	146 (69.5)	61 (29.1)	0	3 (1.4)	0	210[c]
2L	718 (60.9)	442 (37.5)	3 (0.3)	15 (1.3)	1 (0.1)	1,179[a]
2S	476 (59.7)	300 (37.6)	9 (1.1)	8 (1.0)	4 (0.6)	797[a]
3L	1,250 (64.6)	668 (34.5)	2 (0.1)	11 (0.6)	4 (0.2)	1,935[a]
3S	127 (55.5)	91 (39.7)	3 (1.3)	8 (3.5)	0	229
	132 (72.1)	45 (24.6)	0	6 (3.3)	0	183[c]
4L	747 (67.9)	335 (30.5)	8 (0.7)	10 (0.9)	1 (0.1)	1,100[a]
5S	127 (70.6)	48 (26.7)	5 (2.7)	0	0	180[c]
6S	124 (68.5)	53 (29.3)	3 (1.7)	0	1 (0.5)	181[c]
7S	92 (73.6)	30 (24.0)	2 (2.4)	0	0	125[c]

[a] Singh and Tsuchiya (1977); 2x+1 telo selfed (F_2)
[b] Fedak and Helgason (1970)
[c] Two-row with SE16 background

Table 2. Measurements of various plant parts of ditelotetrasomics for 2S, 5S, 6S, and 7S, related telotrisomics, and diploid sibs of barley

Plant parts	Culm length (cm)	Flag leaf		Second leaf		Spike length (cm)	Awn length (cm)	No. spikelets per spike	Glume Awn (mm)	Rachilla (mm)
		Length (cm)	Width (mm)	Length (cm)	Width (mm)					
2x	90.2	18.7	11.0	31.9	14.5	7.7	16.3	26.5	7.0	3.5
2x+1 telo 2S	82.1	18.8	9.5	28.5	13.5	7.7	11.1	24.8	6.3	3.8
2x+2 telo 2S	34.6	11.8	7.0	19.2	9.5	4.9	6.3	15.7	5.0	3.0
2x	75.3	21.0	15.8	33.6	18.7	8.5	17.8	31.4	7.7	3.3
2x+1 telo 5S	74.4	20.2	17.1	30.7	19.9	7.9	17.2	29.2	6.8	3.0
2x+2 telo 5S	70.7	20.6	18.5	29.9	20.0	7.5	14.3	25.8	6.5	2.5
2x	82.2	22.3	13.9	32.8	18.0	8.5	16.4	28.6	6.5	2.7
2x+1 telo 6S	81.5	23.9	17.6	36.4	20.0	8.7	14.1	27.8	7.4	3.1
2x+2 telo 6S	81.7	15.5	13.2	28.0	17.8	6.8	12.6	20.8	6.6	3.0
2x	69.0	19.2	12.4	27.1	14.8	6.8	15.9	23.0	6.0	2.7
2x+1 telo 7S	64.8	16.8	10.6	25.2	13.8	6.0	16.0	22.0	6.1	2.2
2x+2 telo 7S	60.7	12.1	8.9	22.7	12.4	6.6	14.8	20.2	5.5	3.1

The transmission of the extra chromosomes in the selfed progenies of the ditelotetrasomics for 5S, 6S, and 7S was studied. Male and female transmission rates were calculated based on the frequency of the ditelotetrasomic plants in the selfed progenies.

Somatic chromosomes were studied using the acetocarmine squash method (Tsuchiya 1971 b) and Giemsa-banding technique (Singh and Tsuchiya 1982 b). Meiotic chromosome behavior was also studied with the acetocarmine squash method, by analyzing sporocytes from diakinesis through the quartet stages.

Results

Plant morphology

Most of the ditelotetrasomics showed almost no qualitative differences from their related telotrisomics and the diploid sibs, except for ditelotetrasomic 2S (Table 2, Fig. 1). Morphological differences were reported between telotrisomic 2S and its related diploid sibs (Singh

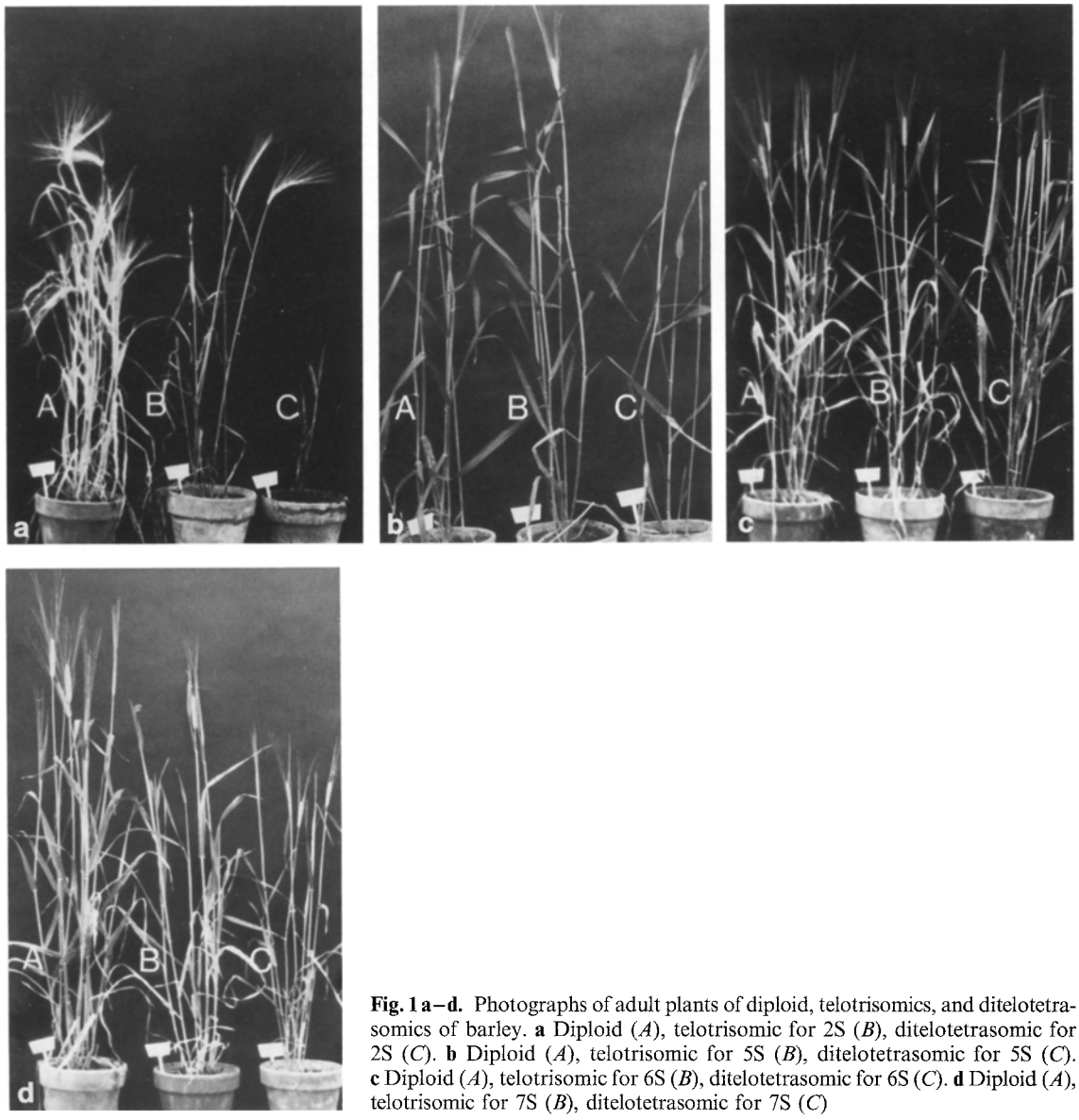

Fig. 1 a–d. Photographs of adult plants of diploid, telotrisomics, and ditelotetrasomics of barley. **a** Diploid (*A*), telotrisomic for 2S (*B*), ditelotetrasomic for 2S (*C*). **b** Diploid (*A*), telotrisomic for 5S (*B*), ditelotetrasomic for 5S (*C*). **c** Diploid (*A*), telotrisomic for 6S (*B*), ditelotetrasomic for 6S (*C*). **d** Diploid (*A*), telotrisomic for 7S (*B*), ditelotetrasomic for 7S (*C*)

and Tsuchiya 1977). Ditelotetrasomic 2S showed enhanced expression of the diagnostic characteristics of telotrisomic 2S. It had narrower, shorter, and darker green leaves, shorter culms and awns, and long rachis internodes. The plants were weak and grew very slowly with only few tillers.

Ditelotetrasomic 5S was very similar to the related triplo 5S and diploid sibs. However, it grew slowly and produced fewer tillers (Fig. 1 b). Its spikes and awns were shorter with long rachis internodes (Table 2). Fused-leaf (onion leaf) trait was observed frequently in ditelotetrasomic 5S plants, especially at later growing stages and on late tillers. This characteristic was also observed in triplo 5S less frequently but not in diploid sibs.

Ditelotetrasomic 6S plants were almost as vigorous as triplo 6S and diploid sibs (Fig. 1 c). However, they grew slowly and the mature plants had shorter flag leaves, spikes, and awns, with fewer spikelets in each spike, and shorter peduncles. Some spikes failed to extrude from the flag leaf sheath (Table 2).

Ditelotetrasomic 7S grew slower than telotrisomic 7S and diploid sibs (Fig. 1 d). During the entire growing period, ditelotetrasomic 7S had softer stems and leaves. The mature plants had shorter flag leaves, awns, and glume awns. No other differences were observed (Table 2).

Somatic chromosome studies

All ditelotetrasomics were derived from selfed progenies of telotrisomics (Table 1). Somatic metaphase chromosomes clearly showed $2n = 14 + 2$ telocentrics (Fig. 2).

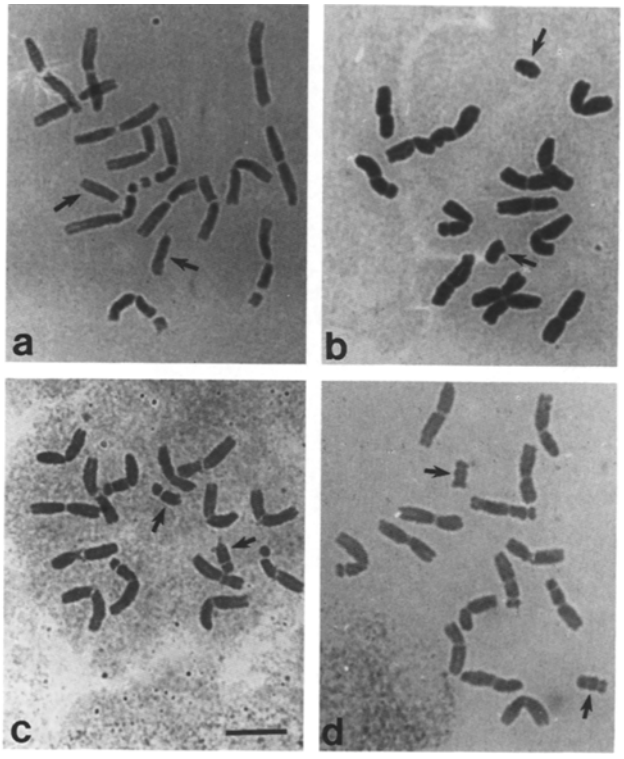

Fig. 2a–d. Somatic metaphase chromosomes in root-tip cells of four ditelotetrasomics. **a** Ditelotetrasomic for 2S. **b** Ditelotetrasomic for 5S. **c** Ditelotetrasomic for 6S. **d** Ditelotetrasomic for 7S. *Bar* represents 10 μm. *Arrow* indicates the telocentric chromosomes

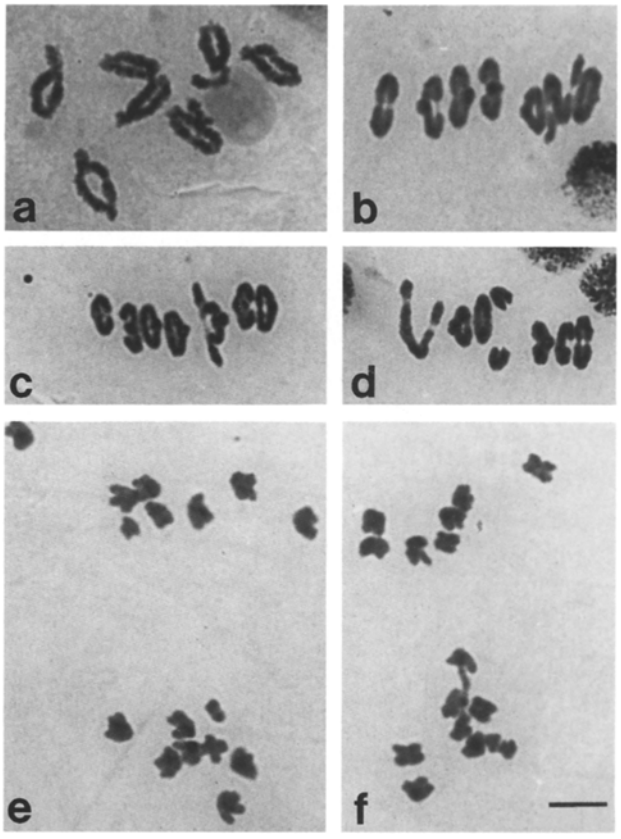

Fig. 3a–f. Meiosis in ditelotetrasomic for 6S of barley. **a** Diakinesis, 6II + 1IV. **b–d** Metaphase I, 6II + 1IV. **e** Anaphase I with 8–8 separation. **f** Anaphase I with 7–9 separation. *Bar* represents 10 μm

Ditelotetrasomics 6S (Fig. 2c) and 7S (Fig. 2d) were easily identified by their obvious satellites. Ditelotetrasomics 2S (Fig. 2a) and 5S (Fig. 2b) were preidentified as they appeared in the progenies of triplo 2S and triplo 5S, respectively, and through the Giemsa-banding technique.

Meiotic chromosome behavior

Meiotic chromosomes were studied at diakinesis and through the quartet stages. Ditelotetrasomic 2S was too weak and had only rudimentary anthers. Thus, meiosis was studied in three ditelotetrasomic types for 5S, 6S, and 7S.

At diakinesis, the two telocentric chromosomes appeared mainly as members of quadrivalents, by association with two homologous normal chromosomes, as $6_{II}+1_{IV}$ (Fig. 3a) or as the two extra telocentrics forming a bivalent with configuration $7_{II}+1$ telo$_{II}$, or as one telocentric chromosome associated with two homologous primary chromosomes to form a trivalent (the other telocentric remaining as univalent), resulting in $6_{II}+1_{III}+1$ telo$_{I}$. Only a small percentage of cells showed a chromosome configuration of $7_{II}+2$ telo$_{I}$ in which the two telocentric chromosomes remained as univalents at this stage (Table 3).

Four types of chromosome configuration observed at diakinesis could also be observed at metaphase I, although at lower frequencies. The percentages of sporocytes with $6_{II}+1_{IV}$ (Fig. 3b–d) and 8_{II} ($7_{II}+1$ telo$_{II}$) decreased, and the percentages of sporocytes with $6_{II}+1_{III}+1$ telo$_{I}$ and $7_{II}+2$ telo$_{I}$ increased (Table 3). In general, from diakinesis to metaphase I, the percentage of univalents increased as a result of chiasma terminalization and precocious separation of the telocentrics. The average frequencies of sporocytes with $6_{II}+1_{IV}$, 8_{II} ($7_{II}+1$ telo$_{II}$), $6_{II}+1_{III}+1$ telo$_{I}$, and $7_{II}+2$ telo$_{I}$ were 58.8, 12.0, 22.3, and 14.8%, respectively (Table 3).

At anaphase I most sporocytes showed 8-8 chromosome separation, with an average frequency of 80% at this stage (Fig. 3e, Table 4). About 4% of the sporocytes showed 7–9 chromosome separation (Fig. 3f, Table 4), in which two telocentric chromosomes displayed nondisjunction and went to the same pole. Some telocentrics had split chromatids at this stage, which usually resulted in laggards. The sporocytes with one and two or more

Table 3. Chromosome association at diakinesis and metaphase I of ditelotetrasomics of barley (numbers in parentheses are percentages)

Ditelotetrasomic		$6_{II}+1_{IV}$	$7_{II}+1_{II}$ [a]	$6_{II}+1_{III}+1_{I}$	$7_{II}+2_{I}$	No. of cells studied
Ditelo 5S	DK [b]	62 (54.4)	36 (31.6)	12 (10.5)	4 (3.5)	114
	MI	92 (36.1)	38 (14.9)	72 (28.2)	53 (20.8)	255
Ditelo 6S	DK	115 (68.4)	43 (25.6)	8 (4.8)	2 (1.2)	168
	MI	221 (64.4)	39 (11.4)	64 (18.7)	19 (5.5)	343
Ditelo 7S	DK	83 (69.2)	25 (20.8)	9 (7.5)	3 (2.5)	120
	MI	109 (51.9)	21 (10.0)	42 (20.0)	38 (18.1)	210

[a] The bivalent of telocentric chromosomes
[b] DK – Diakinesis; MI – Metaphase I

Table 4. Separation of chromosomes at anaphase I and telophase I of three ditelotetrasomics of barley (numbers in parentheses are percentages)

Ditelo-tetrasomic	Anaphase I						Telophase I			
	Normal		One laggard	Two or more laggards	Bridge	No. of cells examined	Normal separation	One laggard	Two ore more laggards	No. of cells examined
	8–8	7–9								
Ditelo 5S	118 (72.0)	3 (1.8)	17 (10.4)	24 (14.6)	2 (1.2)	164	288 (86.3)	22 (6.6)	24 (7.1)	334
Ditelo 6S	134 (88.1)	8 (5.3)	3 (2.0)	5 (3.3)	2 (1.3)	152	133 (91.7)	9 (6.2)	3 (2.1)	145
Ditelo 7S	146 (78.0)	8 (4.3)	7 (3.7)	16 (8.6)	10 (5.4)	187	295 (91.3)	15 (4.6)	13 (4.1)	323

Table 5. Frequency of sporocytes with or without lagging chromosome at anaphase II to telophase II and micronuclei in quartets with three ditelotetrasomics of barley (numbers in parentheses are percentages)

Ditelo-tetrasomic	Frequency of sporocytes at AII to TII with				Frequency of quartets with			
	Normal separation	One laggard	Two or more laggards	No. of cells examined	Normal separation	One micro-nucleus	Two or more micronuclei	No. of cells examined
Ditelo 5S	205 (90.3)	16 (7.1)	6 (2.6)	227	591 (95.8)	19 (3.1)	7 (1.1)	617
Ditelo 6S	503 (94.6)	13 (2.4)	16 (3.0)	532	644 (94.9)	26 (3.8)	9 (1.3)	679
Ditelo 7S	314 (82.6)	38 (10.0)	28 (7.4)	380	740 (93.2)	38 (4.8)	16 (2.0)	794

laggards were observed on the average in 5.4 and 8.8% of the sporocytes, respectively, and about 3% of the sporocytes had bridges (Table 4). The frequency of sporocytes with or without lagging chromosomes at telophase I is shown in Table 4. The normal separation occurred on the average in 89.9% of the sporocytes, ranging from 86.5 to 91.7%. Approximately 10% of the sporocytes showed one or more laggards.

At anaphase II through telophase II, 89.2% of the sporocytes showed normal separation. Approximately 11% of the sporocytes had lagging chromosomes. Most sporocytes (94.9%) showed normal separation of chromosomes at the quartet stage (Table 5). The average frequency of the quartets with one micronucleus was 3.9% and the frequency of those with two or more micronuclei was 1.5%.

Pollen and seed fertility

In general, compared with their related telotrisomic and diploid sibs, the pollen fertility of ditelotetrasomics was fairly high, except for ditelotetrasomic 2S, which was very weak and did not develop normal pollen (Table 6). However, the seed fertility of three ditelotetrasomics was lower than their related telotrisomics and diploid sibs (Table 6); it also varied in different environments. High temperature (35 °C and above) during seed setting reduced seed fertility significantly, especially in ditelotetra-

somic 6S, which was almost sterile at this temperature. The data in Table 6 are from the plants grown in the most favorable environments.

Transmission rates of extra telocentric chromosomes

Transmission rates of two extra telocentric chromosomes were studied in the selfed progenies of ditelotetrasomics. Diploids (2n=14), telotrisomics (2n=14+1 telo), ditelotetrasomics (2n=14+2 homologous telos), and primary trisomics (2n=15) were obtained in selfed progenies of ditelotetrasomics (Table 7). The avarage frequency of ditelotetrasomic plants in the selfed progenies of three ditelotetrasomics (for 5S, 6S, and 7S) was approximately 30% (Table 7). On the average, 84.1% of the selfed progenies had one or two extra telocentric chromosomes, with a range of 79.8 to 92.9%. These data indicate a very high transmission rate of the extra telocentrics in the selfed progenies. Female or male transmission rates were not studied separately. However, at least 30% of pollen transmission of telocentric chromosomes must have occurred, as 30% of ditelotetrasomics were observed in the selfed progenies. Female transmission rate of the extra telocentric chromosomes was estimated at maximum 68%.

Table 6. Pollen and seed fertility of ditelotetrasomics, related telotrisomics, and diploid sibs of barley

Materials	Pollen fertility average (range)	Seed fertility average (range)
Ditelotetra 2S	2.0	0.0
Triplo 2S	93.6 (92.7–94.7)	87.1 (75.0– 94.1)
Diploid sib	96.2 (94.9–97.7)	94.3 (88.9–100)
Ditelotetra 5S	91.6 (87.6–95.1)	65.1 (50.0– 77.8)
Triplo 5S	95.5 (93.1–96.9)	80.0 (73.3– 86.7)
Diploid sib	98.2 (97.0–98.6)	94.9 (87.9–100)
Ditelotetra 6S	91.1 (88.4–95.9)	73.2 (60.0– 85.0)
Triplo 6S	94.2 (93.9–94.5)	88.9 (82.1– 92.9)
Diploid sib	97.2 (95.7–98.7)	99.2 (96.6–100)
Ditelotetra 2S	92.6 (91.7–93.6)	84.2 (80.0– 91.3)
Triplo 2S	93.2 (91.8–96.3)	96.4 (94.7–100)
Diploid sib	97.2 (96.6–98.1)	96.7 (90.5–100)

Discussion

The occurrence of ditelotetrasomic plants in the progenies of telotrisomic plants has been reported by Singh and Tsuchiya (1977) in barley. No ditelotetrasomic plant has been reported in other materials such as *Datura,* tomato, or maize, although some secondary trisomics that were cytogenetically identical to ditelotetrasomics were obtained in the progenies of telotrisomics (Khush 1973).

At present, 11 out of a possible 14 telotrisomics have been established in barley (Tsuchiya 1986). Several hundred plants have been cytologically studied in each of these 11 telotrisomics. Ditelotetrasomic plants occurred in the progenies of only three telotrisomics for long arms (2L, 3L, and 4L). The ditelotetrasomics for 2L and 3L did not reach maturiy, while those for 4L grew to maturity. Telocentric chromosome 4L, however, was found to have 32% distal deficiency (Singh and Tsuchiya 1982a). On the other hand, six known telotrisomics for the short arm (1S, 2S, 3S, 5S, 6S, and 7S) produced ditelotetrasomic plants in their selfed progenies. All six ditelotetrasomics were viable and grew to maturity. With the exception of the ditelotetrasomic for 2S, all ditelotetrasomics for short arms showed varied degrees of pollen and seed fertility (Table 6), and transmitted ditelotetrasomics in their selfed progenies (Table 7).

The frequency of different ditelotetrasomics from selfed telotrisomics ranged from 0.1 to 2.7% (Table 1). The average frequency of ditelotetrasomics for three long arms (2L, 3L, and 4L) was 0.31%, while that of six telotrisomics for short arms (1S, 2S, 3S, 5S, 6S, and 7S) was 1.09%. However, in the two-rowed type (*VV*) of SE16 background, ditelotetrasomic plants were obtained in only seven out of the nine telotrisomic types (2L, 2S, 3L, 4L, 5S, 6S, and 7S); the ditelotetrasomic plants of 1S and 3S were all derived from six-rowed plants (Wang and Tsuchiya 1989).

It was reported that all telotrisomic plants for the long arms of barley chromosomes showed diagnostic characteristics similar to their related primary trisomics (Fedak et al. 1971; Tsuchiya 1971a; Singh and Tsuchiya 1977). Detailed studies of plant morphology showed that

Table 7. Transmission rates of telocentric chromosomes in the selfed progenies of ditelotetrasomics of barley (numbers in parantheses are percentages)

Ditelotetrasomic	Chromosome number					Total no. of plants
	14	14+1telo	14+2telos	15	Other	
Ditelotetra 5S	19 (16.7)	58 (50.9)	33 (28.9)	1 (0.8)	3 (2.6)	114
Ditelotetra 6S	7 (5.5)	81 (63.8)	37 (29.1)	2 (1.6)	0	127
Ditelotetra 7S	30 (20.3)	72 (48.6)	46 (31.1)	0	0	148

the ditelotetrasomic plants for the short arms of barley chromosomes were, in general, qualitatively similar to their parental telotrisomics and diploid sibs, with the exception of ditelotetrasomic 2S plants (Singh and Tsuchiya 1977; Wang and Tsuchiya 1990). The difference between long arm and short arm on the plant character expression in the telotrisomics has been studied by aneuhaploid analysis (Tsuchiya and Shahla 1983; Furuta and Tsuchiya 1987, 1991). Based on the results from telotrisomics, ditelotetrasomics, and aneuhaploids, Tsuchiya (1991) proposed that developmental genetic or morphogenetic element(s) may exist which are different from Mendelian genetic element and which control the developmental or morphogenetic processes when genetic balance is disturbed.

From diakinesis to metaphase I (MI), the frequency of sporocytes with $6_{II}+1_{IV}$ and $7_{II}+1$ telo$_{II}$ chromosome configurations was reduced in all three types of ditelotetrasomics, due to chiasma terminalization and precocious separation. This is in agreement with the results obtained in simple primary trisomics (Tsuchiya 1960, 1967) and in 11 telotrisomics (Singh and Tsuchiya 1981; Wang and Tsuchiya 1990). Correspondingly, the frequency of sporocytes with $6_{II}+1_{III}+1$ telo$_{I}$ and $7_{II}+2$ telo$_{I}$ chromosome configurations increased from diakinesis to metaphase I (Table 3). At MI, $6_{II}+1_{III}$ chromosome configuration was predominant in telotrisomics (Singh and Tsuchiya 1981; Wang and Tsuchiya 1990). Similarly, the $6_{II}+1_{IV}$ configuration was in the majority among different chromosome configurations at MI in ditelotetrasomics. This indicates that extra telocentrics tend to stay associated with their homologous normal chromosomes.

Except for ditelotetrasomic 2S, the ditelotetrasomics in this study showed good pollen fertilities, with an average of 91.8% (Table 6). It has been reported that an extra telocentric chromosome does not have a harmful effect on pollen fertility in barley (Singh and Tsuchiya 1977; Wang and Tsuchiya 1990). The meiotic study indicated that ca. 80% or more sporocytes showed 8-8 separation at AI (Table 4) and normal behavior at later stages (Tables 4 and 5). Thus, the majority of gametes formed could contain one extra telocentric chromosome (7+1 telocentric). This suggested that an extra telocentric for the short arm did not have a harmful effect on pollen fertility.

Compared to pollen fertility, seed fertility was relatively low in three lines of ditelotetrasomics, ranging from 73.2 to 84.2% (Table 6). This indicated either that two extra telocentric chromosomes had some degree of negative effect on seed formation or that pollen with an extra telocentric is less competitive in fertilization. According to the present authors' observation, ditelotetrasomic plants reacted more sensitively in their seed fertility than their related telotrisomics and diploid sibs in certain environments (such as high temperature).

It is important to note that ditelotetrasomics had high transmission rates of extra telocentric chromosome(s). The extra telocentric transmitted averaged 84% progenies through selfing ranging from 78.7 to 92.9% (Table 7). The average female and male transmission rates are roughly calculated as maximum 68 and 46%, respectively. These values are much higher than those of telotrisomics, in which the average female and male transmission rates of the extra telocentric chromosome were 30.7 and 2%, respectively (Singh and Tsuchiya 1977; Wang and Tsuchiya 1990). This suggested that ditelotetrasomics could be a useful material in the genetic analysis of linkage mapping; the high transmission rate would greatly increase the efficiency of telotrisomic F_1 production.

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