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Cytogenetics of four telotrisomics in barley (*Hordeum vulgare* L.)*

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Summary. Four barley telotrisomics (Triplo 3S, 5S, 6S, and 7S) were studied. No major qualitative differences in morphology between the telotrisomics and their diploid sibs were found. The pollen and seed fertility of these telotrisomics was comparable to their diploid sibs. The meiotic study showed that the average frequency of $6_{II}+1_{III}$ at diakinesis and metaphase I was 84.2% and 71.7%, respectively. The normal chromosome separation ranged from 77.2% to 89.4% at anaphase I through telophase II. The transmission rate of the extra telocentric chromosomes averaged 28.4% upon selfing and 28.7% through the female. All four telotrisomics showed various degrees of pollen transmission, the average being 3.6%. Ditelotetrasomic plants (2n=14+2 homologous telocentrics) were obtained in the progenies of selfed monotelotrisomic plants of all four types. These ditelotetrasomic plants were viable and showed various degrees of seed fertility.

Key words: Telotrisomics – Barley – Morphology – Cytology – Transmission

Introduction

The telosomic trisomic or telotrisomic plant is the trisomic with extra telocentric chromosome, in addition to the normal diploid chromosome complement (Burnham 1962; Khush and Rick 1968). Telotrisomics have been reported in some diploid species such as tomato (Khush and Rick 1968), diploid wheat (Smith 1947), maize (Rhoades 1936, 1938, 1940), tobacco (Goodspeed and Avery 1939), and others (Khush 1973). The telotrisomics in barley were reported first by Tsuchiya (1969) and later by Fedak et al. (1971, 1972, Singh and Tsuchiya 1977, 1981a, 1982), Tsuchiya (1971a, 1972a, 1972b), and Tsuchiya and Singh (1982). Eleven telotrisomics have been obtained from various sources and established in cultivar SE16 background (Singh and Tsuchiya 1982; Furst and Tsuchiya 1983; Shahla and Tsuchiya 1982, 1984). Table 1 lists proposed and previous designation of all these telotrisomics in barley. These telotrisomics have been widely used in associating genes with chromosome arms, locating the centromere position in genetic linkage

Table 1. Proposed and previous designation of eleven telotrisomics in barley

Proposed designation	Previous designation	
	Tsuchiya 1971a	Tsuchiya 1972c; Singh and Tsuchiya 1977, 1981a Tsuchiya and Singh 1982
Triplo 1L	Telotri 1L	Triplo 1L
Triplo 1S	Telotri 1S	Triplo 1S
Triplo 2L	Telotri 2L	Triplo 2L
Triplo 2S	Telotri 2S	Triplo 2S
Triplo 3L	Telotri 3A	Triplo 3S
Triplo 3S[a]		
Triplo 4L	Telotri 4A	Triplo 4S
Triplo 5L	Telotri 5A	Triplo 5L
Triplo 5S[b]		
Triplo 6S[c]		
Triplo 7S[d]		

[a] Singh and Tsuchiya (1981b)
[b] Furst and Tsuchiya (1983); Shahla and Tsuchiya (1984)
[c] Seip (1980)
[d] Shahla and Tsuchiya (1982)

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maps, and determining gene order in the chromosome arm (Tsuchiya and Singh 1982; Tsuchiya 1983, 1986; Shahla and Tsuchiya 1990). Seven telotrisomics in barley (1L, 1S, 2L, 2S, 3L, 4L, and 5L) have been reported in detail (Singh and Tsuchiya 1977, 1981 a). This paper reports the results of cytogenetic studies of additional four telotrisomics (3S, 5S, 6S, and 7S).

Table 2. Sources of telotrisomics of barley

Designation	Original variety	Source
Triplo 3S	Shin Ebisu 16 (SE16)	Acrosomic trisomic $3L^{3S}$
Triplo 5S	Shin Ebisu 16 (SE16)	Primary trisomic, Triplo 5
Triplo 6S	Shin Ebisu 16 (SE16)	Primary trisomic Triplo 6
Triplo7S	Shin Ebisu 16 (SE16)	Primary trisomic, Triplo 7

Materials and methods

The four telotrisomics were obtained in the progenies of related aneuploid plants (Table 2).

Morphological measurements were made on full-grown plants to compare the four telotrisomics with their diploid sibs. The main culm was used for all measurements. Pollen grains were stained with diluted acetocarmine and analyzed based on Kihara's (1937) classification; pollen grains with two well-developed sperm nuclei and a vegetative nucleus were considered functional pollen grains and others were abortive or empty grains.

Somatic chromosomes were studied with the acetocarmine squash method (Tsuchiya 1971 b) and Giemsa N-banding technique (Singh and Tsuchiya 1982). Meiotic cells were also studied with the acetocarmine squash technique.

Table 3. Measurements of various plant parts of Triplo 3S, Triplo 5S, Triplo 6S, Triplo 7S, and diploid control

Plant parts	2x	2x+3S	2x	2x+5S	2x	2x+6S	2x	2x+7S
Culm length (cm)	118.0	94.2	102.8	101.5	116.1	116.8	100.5	86.6
Leaf length (cm)[a]	30.1	31.1	30.9	27.2	27.4	28.7	29.5	27.9
Leaf width (mm)[a]	2.1	2.4	1.8	1.7	1.6	1.8	1.7	1.5
Flag leaf length (cm)	15.8	19.6	16.4	14.7	14.3	16.4	19.2	17.5
Flag leaf width (mm)	1.8	1.8	1.5	1.3	1.3	1.5	1.4	1.2
Spike length (cm)	9.5	9.5	7.5	7.5	8.3	8.0	7.1	7.2
Awn length (cm)	14.0	13.0	15.6	14.6	16.9	14.3	13.8	13.8
No. spikelets/spike	22.5	21.8	28.5	27.3	32.0	28.3	28.0	23.3
Glum awn length (mm)	9.3	8.3	6.3	5.5	5.8	7.0	4.5	4.1
Rachilla length (mm)	4.4	4.2	4.1	3.8	3.8	3.9	3.0	3.7

[a] Second leaf from the top (flag) leaf

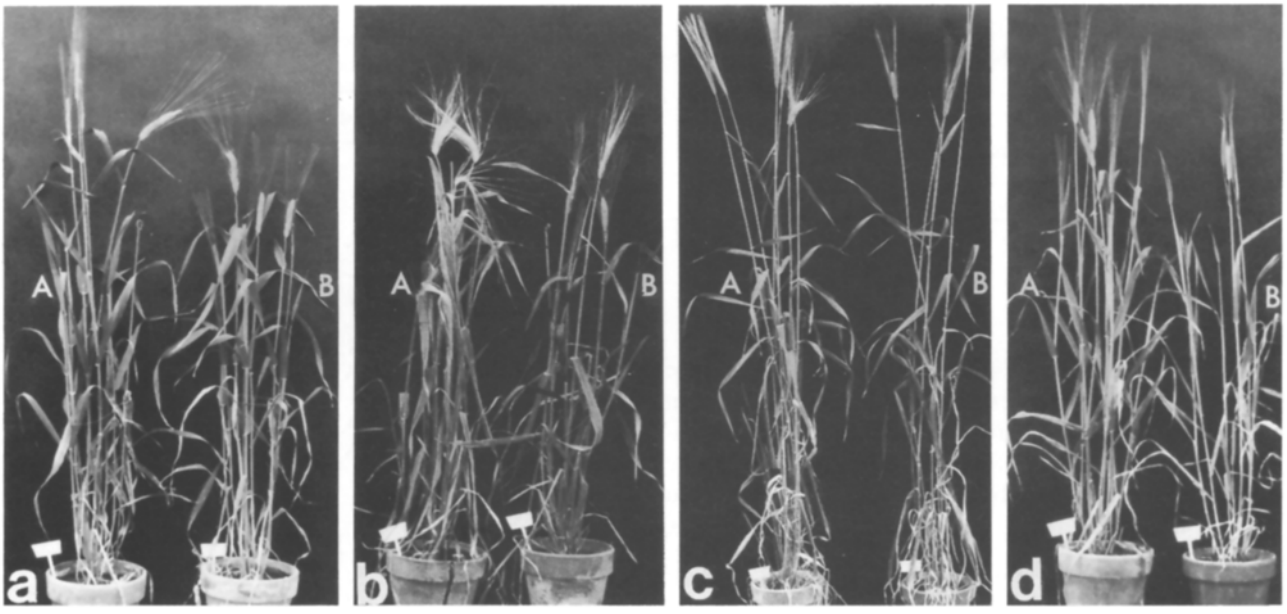

Fig. 1 a–d. Morphology of adult plants of the telotrisomics (*B*) and their diploid sibs (*A*). **a** Diploid sib and Triplo 3S; **b** Diploid sib and Triplo 5S; **c** Diploid sib and Triplo 6S; **d** Diploid sib and Triplo 7S

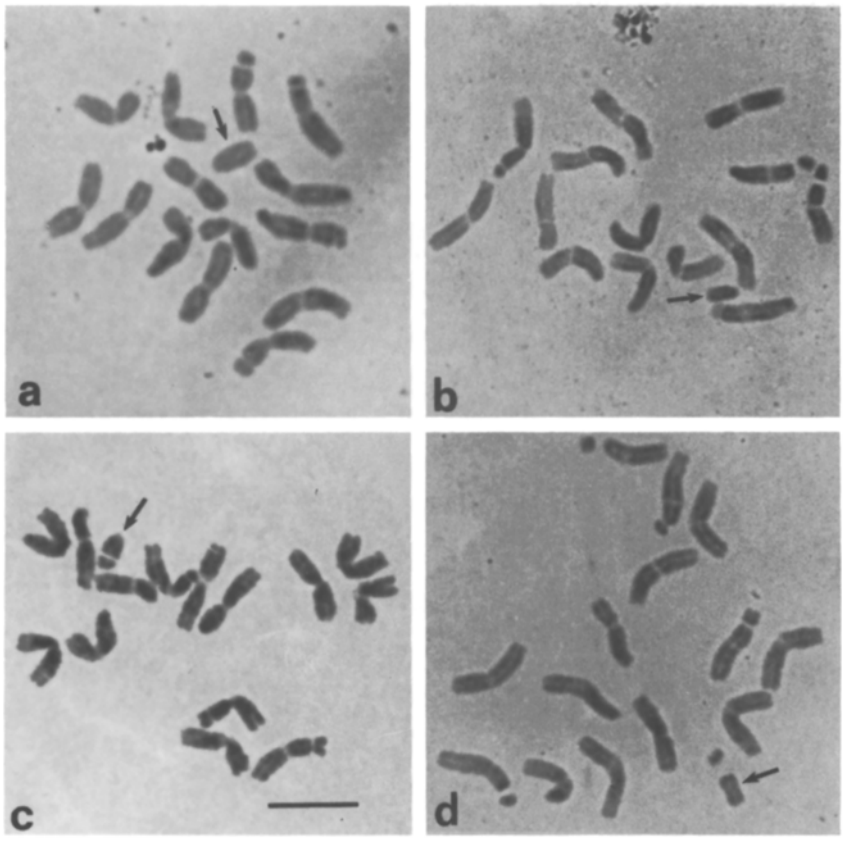

Fig. 2a–d. Somatic metaphase chromosomes in root-tip cell of four telotrisomics. **a** 14+1 telo 3S; **b** 14+1 telo 5S; **c** 14+1 telo 6S; **d** 14+1 telo 7S. *Bar* represents 10 μm. *Arrow* indicates the telocentric chromosome

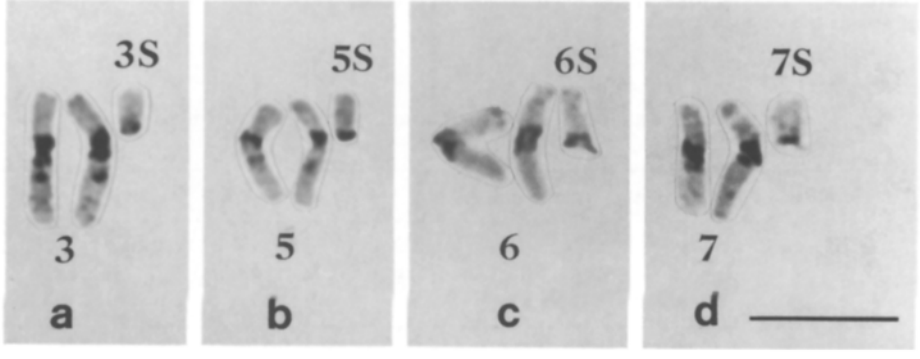

Fig. 3a–d. Giemsa N-banded telocentric chromosomes together with a pair of corresponding primary chromosomes of four telotrisomics. **a** Telosome 3S; **b** Telosome 5S; **c** Telosome 6S; **d** Telosome 7S. *Bar* represents 10 μm

Results

Morphology

The four telotrisomics matured later than diploid sibs, but all were either quite similar or showed minor variations in very minor morphological characteristics (Fig. 1, Table 3). Triplo 3S had shorter culms than the diploid sibs but was very similar in all other characteristics. Compared with diploid sibs, Triplo 5S had slightly darker and shorter leaf blades. Triplo 6S had almost the same vigor as diploid sibs, but showed thicker stems and wider leaf blades with slightly darker green color. Triplo 7S was less vigorous than diploid sibs and had slower growth and shorter culms. However, differences were rather small in most cases. It was rather difficult to identify the telotrisomics from their diploid sibs without careful morphological and cytological observations.

Somatic chromosome

Somatic chromosomes studied with the acetocarmine technique did not show enough differences to identify the telocentric 3S (Fig. 2a). The telocentric 5S was identified with the acetocarmine squash technique due to its smallest size of all 14 chromosome arms (Fig. 2b). Telocentrics 6S (Fig. 2c) and 7S (Fig. 2d) were clearly identified with the acetocarmine squash methods by their char-

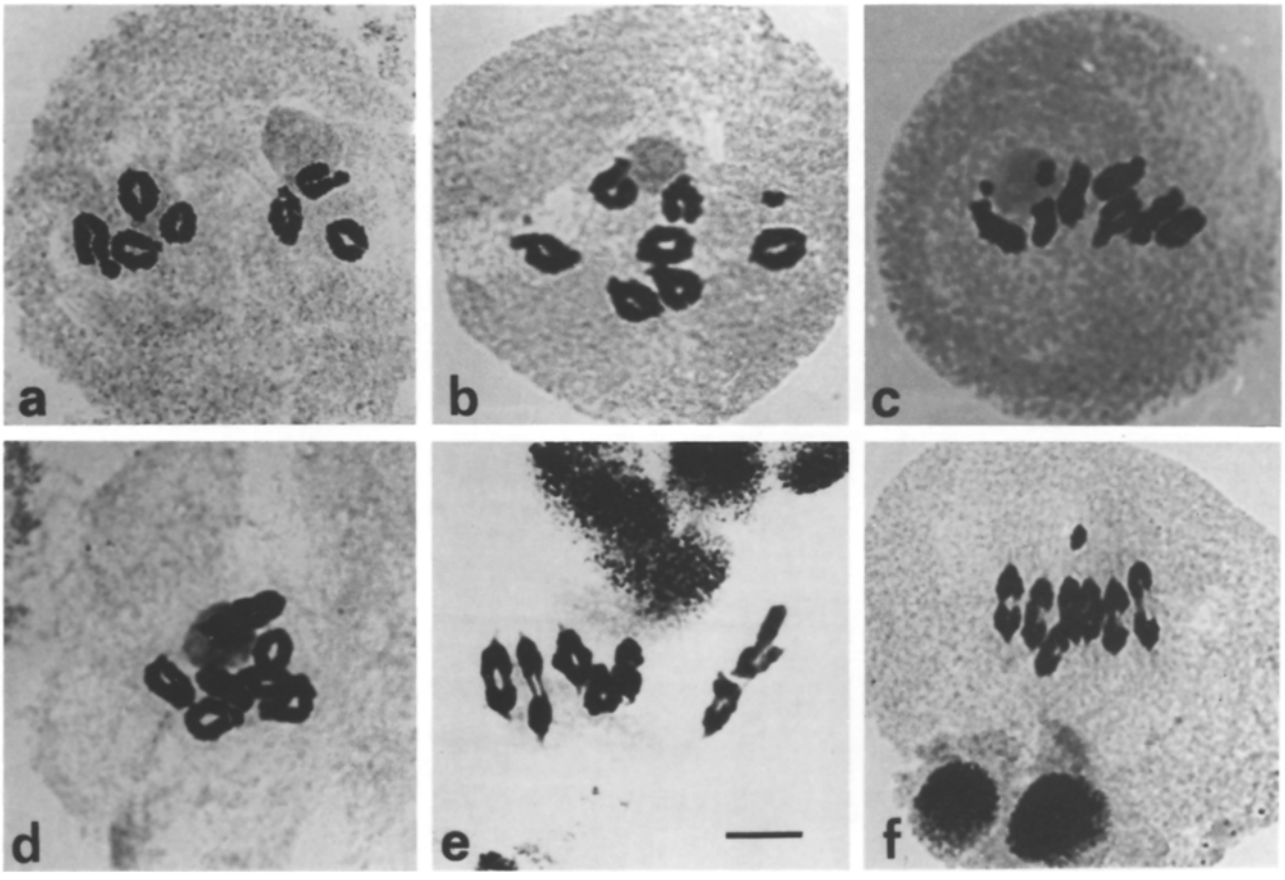

Fig. 4a–f. Meiosis in telotrisomics in barley. **a–d** Diakinesis. **a** Triplo 3S; **b** Triplo 5S; **c** Triplo 6S; **d** Triplo 7S; **e–f** Metaphase I. **e** Triplo 6S; **f** Triplo 7S. *Bar* represents 10 μm

Table 4. Chromosome associations at diakinesis and metaphase I and separation of chromosome at anaphase I in four telotrisomics of barley (%)

Telo-trisomic type	Diakinesis			Metaphase I			Anaphase I					
	1 III +6 II	7 II +1 I	No. cells studied	1 III +6 II	7 II +1 I	No. cells studied	7–8 separation	One laggard	Two laggards	7+1 – 7+1 separation	Bridge	No. cells studied
Triplo												
3S	86.8	13.2	121	70.6	29.5	163	82.5	10.3	4.1	2.1	1.0	97
5S	81.1	18.9	111	72.3	27.7	173	78.0	12.0	7.6	1.2	1.2	250
6S	79.6	20.4	201	72.6	27.4	157	73.9	10.2	9.1	4.0	2.8	176
7S	89.1	10.9	147	71.4	28.6	175	74.3	11.4	10.7	2.2	1.4	140
Average (Total)	84.2	15.8	580	71.7	28.3	668	77.2	11.0	8.0	2.4	1.6	663

acteristic satellites. The telocentric 6S with its larger satellite was easy to distinguish from 7S, which had a smaller satellite.

Giemsa N-banding method clearly showed unique characteristics of all four telocentric chromosomes previously identified and designated (Fig. 3). The telocentric 3S showed a large band block at the centromere area (Fig. 3a). The telocentric 5S showed a centromeric band (Fig. 3b). The telocentric 6S also showed a prominent centromeric band and faint dot on the telomere of the satellite (Fig. 3c). The telocentric 7S had a band on the centromere portion and a narrow band was close by. No band or dot was observed on the telomere of the satellite in 7S (Fig. 3d).

Table 5. Types and frequency of trivalents at metaphase I of four telotrisomics of barley (%)

Telo-trisomic type	Types and frequencies of trivalents			No. of cells studied
	Tandem V	Rod	Ring and rod	
Triplo 3S	55.2	23.2	21.6	203
Triplo 5S	53.3	25.8	20.9	124
Triplo 6S	55.5	21.9	22.6	128
Triplo 7S	47.9	23.7	28.4	186
Average (Total)	52.9	23.7	23.4	641

Meiotic chromosome behavior

Meiotic chromosomes were studied from diakinesis through the quartet stage. Early meiotic stages were not analyzed due to lack of distinguishing features (Singh and Tsuchiya 1975).

Diakinesis. At this stage, the telocentric chromosomes appeared either as members of a trivalent by association with two homologous primary chromosomes as $6_{II}+1_{III}$ (Fig. 4a, c, d) or as univalents, $7_{II}+1_{I}$ (Fig. 4b). The average frequency of the $6_{II}+1_{III}$ configuration was 84.2% (Table 4), ranging from 79.6% in Triplo 6S to 89.1% in Triplo 7S.

Metaphase I. Both $6_{II}+1_{III}$ (Fig. 4e) and $7_{II}+1_{I}$ (Fig. 4f) chromosome configurations were observed at this stage. However, the frequency of the sporocytes having $6_{II}+1_{III}$ decreased with the increasing frequency of those with $7_{II}+1_{I}$. The average frequency of $6_{II}+1_{III}$ and $7_{II}+1_{I}$ for the four telotrisomics was 71.7% and 28.3%, respectively (Table 4). The trivalents appeared in different shapes such as V-shape, rod-shape, and ring-and-rod, with the V shape being the majority (Table 5).

Anaphase I. Most sporocytes showed a 7–8 chromosome separation (Table 4) with an average of 77.2% for the four telotrisomics. About 19% of sporocytes showed lagging chromosomes, with one laggard being in the majority of sporocytes. Approximately 2.4% of the telocentric chromosomes divided at this stage and showed 7+1–1+7 separation. Also about 1.6% of the sporocytes showed bridges at this stage (Table 4).

Telophase I. Sporocytes at this stage showed an average of 89.4% normal separation (Table 6), ranging from 85.0% (Triplo 5S) to 92.1% (Triplo 6S). About 10.6% of the sporocytes had lagging chromosomes.

Second meiotic division. The frequencies of sporocytes at anaphase II to telophase II are shown in Table 6. Sporo-

Table 6. Frequency of sporocytes with or without lagging chromosomes at telophase I to telophase II, and micronuclei in microspore quartets of four telotrisomics of barley (%)

Tele-trisomic type	Frequency of sporocytes at TI with				Frequency of sporocytes at A II to T II with				Frequency of microspore quartets with			
	Normal separation	One laggard	Two laggards	No. cells studied	Normal separation	One laggard	Two laggards	No. cells studies	No micro-nuclei	One micro-nucleus	Two micro-nuclei	No. cells studied
Triplo 3S	89.4	8.5	2.1	97	80.3	17.2	2.5	319	88.3	8.8	2.9	137
5S	85.0	9.0	6.0	100	85.9	6.8	7.3	205	84.9	12.9	2.2	233
6S	92.1	4.3	3.6	139	78.6	14.5	6.9	248	83.0	15.2	1.8	283
7S	91.1	4.1	4.8	169	83.4	13.3	3.3	302	95.0	3.6	1.4	220
Average (Total)	89.4	6.5	4.1	505	82.1	12.9	5.0	1074	87.8	10.1	2.1	873

cytes with normal separation were 78.6% in Triplo 6S to 85.9% in Triplo 5S, the average being 82.1%. Lagging chromosomes were found in 17.9% of the sporocytes.

Quartet stage. The average frequency of normal quartets without a micronucleus was 87.8%, ranging from 83.0% in Triplo 6S to 95.0% in Triplo 7S (Table 6). The average frequency of the occurrence of one and two micronuclei per quartet was 10.0% and 2.1%, respectively.

Pollen and seed fertility

Pollen and seed fertility were relatively high in all four telotrisomics, as shown in Table 7. The pollen fertility for diploid sibs ranged from 97.2% to 97.9%, while the pollen fertility of the four telotrisomics ranged from 92.6% in Triplo 5S to 95.8% in Triplo 3S, with an average of 93.9%, which is very high for aneuploid plants (Table 7).

The seed fertility averaged 95.4% for the diploid sibs (Table 7). Average seed fertility for four telotrisomics was 87.0%, ranging from 73.6% for Triplo 3S to 93.4% for Triplo 6S.

Table 7. Pollen and seed fertility in four telotrisomics of barley

Material	Pollen fertility	Seed fertility
Triplo 3S	95.8	73.6
Diploid sib	97.9	90.0
Triplo 5S	92.6	90.1
Diploid sib	97.8	96.6
Triplo 6S	94.2	93.4
Diploid sib	97.2	98.5
Triplo 7S	93.2	91.0
Diploid sib	97.2	96.6

Table 8. Transmission rates (%) of extra telocentric chromosome in four telotrisomics of barley

Telotrisomic types	Chromosome nos.					No. of plants studied
	14	14+1 telo	14+2 telos	15	Other	
	2x+1 telo selfed					
Triplo 3S	62.5	33.5	0.8	3.2	–	128
Triplo 5S	70.6	26.7	2.7	–	–	180
Triplo 6S	68.5	29.3	1.7	–	0.5[a]	181
Triplo 7S	73.6	24.0	2.4	–	–	125
Average (Total)	68.8	28.4	1.9	0.8	0.1	614
	2x+1 telo × 2x					
Triplo 3S	68.7	30.8	–	0.5	–	201
Triplo 5S	75.3	23.5	–	1.2	–	85
Triplo 6S	67.5	32.2	0.3	–	–	378
Triplo 7S	71.7	28.3	–	–	–	272
Average (Total)	70.0	28.7	0.1	0.4	–	936
	2x × 2x+1 telo					
Triplo 3S	98.8	1.2	–	–	–	81
Triplo 5S	93.3	6.7	–	–	–	42
Triplo 6S	96.4	3.6	–	–	–	56
Triplo 7S	97.3	2.7	–	–	–	73
Average (total)	96.4	3.6	–	–	–	252

[a] The chromosome number was 2n=14+1 acro $6L^{6S}$

Transmission of extra telocentric chromosome

Transmission of extra telocentric chromosomes was studied in the progenies of selfed telotrisomics and the reciprocal crosses between telotrisomics and diploids (Table 8).

Selfed progenies. The average frequency of monotelotrisomics in the selfed progenies for the four telotrisomics was 28.4%, ranging from 24.0% in Triplo 7S to 33.5% in Triplo 3S. Ditelotetrasomic plants (2n=14+2 homologous telos) were obtained in the progenies of all four telotrisomics, with the average frequency of 1.9% and ranging from 0.8% for Triplo 3S to 2.7% for Triplo 5S. All these ditelotetrasomic plants grew normally in the greenhouse, with various degrees of seed fertility. Plants with 15 normal chromosomes (primary trisomics) and 14+1 acro $6L^{6S}$ chromosomes were also obtained in the selfed progenies (Table 8).

Telotrisomics × diploid. The average female transmission rate of the extra chromosome for the four telotrisomics was 28.7%. The transmission rates were similar for the four telotrisomics. A ditelotetrasomic plant was found in the progeny of the cross between Triplo 6S and diploid, which indicated a female transmission of two extra telocentric chromosomes due to nondisjunction of the telosome. A plant with 15 normal chromosomes (primary trisomic) was found in the progenies of Triplo 3S and 5S (Table 8).

Diploid × telotrisomics. The transmission rate of the extra chromosome through male gamete was studied to a limited extent. Transmission of telocentric chromosomes through pollen occurred in all four telotrisomics (3S, 5S, 6S, and 7S), with an average frequency of 3.6% and ranging from 1.2% in Triplo 3S to 6.7% in Triplo 5S. No ditelotetrasomics or plants with 15 normal chromosomes or others were found (Table 8).

Discussion

All simple primary trisomics showed diagnostic morphological characteristics that are different from one another and from diploid sibs, both qualitatively and quantitatively (Tsuchiya 1960, 1967). The telotrisomics for the long arms (Triplo 1L, 2L, 3L, 4L, and 5L) resembled

their corresponding primary trisomics morphologically (Singh and Tsuchiya 1977). However, the Triplo 3S, 5S, 6S, and 7S in this study did not show diagnostic traits similar to their corresponding primary trisomics. Generally, they were only slightly different from their diploid sibs. These results agreed with the observations of the telosomic trisomics for the short arms (1S) of chromosome 1 (Fedak et al. 1971; Tsuchiya 1969, 1971a; Singh and Tsuchiya 1977). Similar observations were reported by Khush and Rick (1968) for the telotrisomics of tomato. It is rather difficult to explain what causes the phenotypic differences between the telotrisomics for long arms and short arms, since all seven short arms of barley chromosomes are genetically not inert, carrying at least one Mendelian gene in each arm (Tsuchiya 1986).

From diakinesis to metaphase I (MI), the frequency of sporocytes with the $6_{II}+1_{III}$ chromosome configuration was reduced in all four telotrisomics, due to the chiasma terminalization. This is in agreement with the results in primary trisomics (Tsuchiya 1960, 1967) and seven other telotrisomics (Singh and Tsuchiya 1981a). Correspondingly, the frequency of sporocytes with $7_{II}+1_{I}$ increased from diakinesis to metaphase I (Table 4).

The frequency of trivalents at diakinesis in Triplo 3S and 5S was 86.8% and 81.1%, respectively (Table 4), which was different from 77.8% and 89.1% in Triplo 3L and 5L (Singh and Tsuchiya 1981a). Since telocentric 5L is longer than telocentric 5S, the 5L should have more physical opportunity for homologous pairing with the corresponding primary chromosome. The results obtained in 5L (Singh and Tsuchiya 1981a) and 5S (this paper, Table 4) agree with the expectation. A similar observation was reported by Singh and Tsuchiya (1981a) between Triplo 1L and 1S. However, in the case of chromosome 3, it seems to be different. Telocentric 3S is shorter than 3L, but there were more sporocytes showing $6_{II}+1_{III}$ at diakinesis in Triplo 3S (86.8%) than in Triplo 3L (77.8%).

The average frequencies of sporocytes with trivalent at diakinesis and metaphase I in these four telotrisomics (Triplo 3S, 5S, 6S, and 7S) were 84.2% and 71.7%, respectively (Table 4), which is higher than the average of 74.6% (diakinesis) and 66.9% (MI) in five telotrisomics for the long arms (Triplo 1L, 2L, 3L, 4L, and 5L) reported by Singh and Tsuchiya (1981a). However, since these materials were grown under different environments, these differences may be ascribed to environmental effects. It seems to be necessary to grow all materials under the same environmental condition to study the effect of opposite arms on trivalent frquency. There may be weak promotor or suppressor genes affecting meiotic chromosome pairing in some barley chromosomes, as observed in wheat (Kimber and Sears 1987).

The study of chromosome behavior at diakinesis showed that the observation of the nucleolus is important when studying Triplo 6S and Triplo 7S. The materials to be used for meiotic study should be stained well enough to show the nucleolus, so that the chromosome configuration and the nucleolus-chromosome relationship at diakinesis could be accurately observed. Otherwise, some trivalents might be judged as a bivalent plus a univalent (Fig. 4c and d). There might be a few sporocytes in which the telocentric chromosomes separated from their corresponding bivalents by nucleolus and were, in fact, univalents. If this occurred in this study, they were counted as trivalents.

All four telotrisomics showed fairly good pollen fertility, with an average of 94.0%. This indicates that an extra telocentric chromosome does not have a harmful effect on pollen fertility.

The female transmission rates of the four telotrisomics were very similar. The transmission rates are higher than those reported for primary trisomics (Tsuchiya 1960, 1967) and similar to those of the other seven telotrisomics (Singh and Tsuchiya 1977). This suggests that the extra telocentric chromosome has a greater opportunity to be physically included in the gamete together with a complete genome to form viable and functional gametes.

It is important to note that ditelotetrasomic plants were obtained in the progenies of four telotrisomics (Table 8). Ditelotetrasomic plants were also reported previously for 1S (Fedak and Helgason 1970; Tsuchiya 1969; Singh and Tsuchiya 1977) and for 2L, 2S, 3L, and 4L (Singh and Tsuchiya 1977). Ditelotetrasomics for 2L and 3L did not survive beyond the seedling stage, however. ditelotetrasomics for 4L were viable, most likely because of a distal deficiency (Singh and Tsuchiya 1982).

The four ditelotetrasomics obtained in this study (for 3S, 5S, 6S, and 7S) were all viable and rather vigorous with various degrees of pollen and seed fertility and showed rather high transmission rates (S. Wang and T. Tsuchiya, unpublished results). These ditelotetrasomics would be useful for stock maintenance and genetic studies in the future.

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