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Spontaneous chromosomal rearrangements in cultivated and wild barleys

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Summary. Four of 1,240 cultivated barley lines collected from different regions of the world and 3 of 120 lines of wild barley, *Hordeum spontaneum* C. Koch, carry spontaneous reciprocal translocations. Breakpoint positions and rearrangements in the interchanged chromosomes have been examined by both test crosses and Giemsa banding techniques. The four translocation lines in cultivated barley were all of Ethiopian origin and have the same translocation involving chromosomes 2 and 4. The breakpoints are at the centromeres of both chromosomes, resulting in interchanged chromosomes 2S+4S and 2L+4L (S=short arm, L=long arm). A wild barley line, Spont.II, also has translocated chromosomes 2 and 4 which are broken at the centromeres. The resultant chromosomes are, however, 2S+4L and 2L+4S. Another wild barley line, Spont.S-4, has interchanged chromosomes with breakpoints in the short arm of chromosome 3 and the long arm of chromosome 7. In addition, this line has a paracentric inversion in the short arm of chromosome 7 that includes a part of nucleolar constriction, resulting in two tandemly arranged nucleolar constrictions. The third wild barley line, Spont.S-7, has interchanged chromosomes with breakpoints in the long arms of both chromosomes 3 and 6. The translocated chromosome 3 is metacentric and the translocated chromosome 6 has a long arm similar in length to the long arm of chromosome 7.

Key words: *Hordeum vulgare* – *Hordeum spontaneum* – Spontaneous chromosomal rearrangement – Reciprocal translocation – Inversion – Giemsa C-banding

Introduction

Chromosomal rearrangements in barley, including reciprocal translocations and inversions, are rare in nature, although they are induced frequently by mutagen treatments (Burnham et al. 1954; Hagberg and Hagberg 1968; Nilan 1964; Ramage et al. 1961; and others). As to spontaneous chromosomal rearrangements, Smith (1941) found a partially sterile mutant caused by a reciprocal translocation in a strain (C.I. 3845) from Kashmir in India, and a "Sterile Flowers" stock caused by a paracentric inversion in a selection from *Hordeum deficiens,* C.I. 2229. Powell and Nilan (1968) examined microsporocytes at late anaphase I of 15 cultivars and their hybrids cytologically, and found one or possibly two small paracentric inversions in 'OAC 21'. Analyses of other hybrids revealed that at least two other cultivars also possessed inversions. Prasad (1976) described paracentric inversions in two lines. Further, Yu and Hockett (1979) obtained cytological evidence for a reciprocal translocation and five inversions in partially sterile plants discovered in the field. According to Ramage (1985), only 12 out of 602 translocation stocks at the University of Arizona were of spontaneous origin.

Recently, in a study on hybrid weakness (Konishi 1985), the senior author found partially sterile F_1 plants between some Ethiopian lines and the tester line, Turkey 193 (Okayama University Accession No. OUT 065). By observing the chromosome configurations in their PMCs, two Ethiopian lines, Debre Zeit 34 (OUE 227) and Sululta 16 (OUE 259), were found to have reciprocal translocations (Konishi and Takahashi 1985).

The finding of spontaneous reciprocal translocations in Ethiopian lines prompted a more detailed

investigation of chromosomal rearrangements in cultivated and wild barleys. The present study aims to: (1) detect the spontaneous reciprocal translocation lines in cultivated and wild barleys; (2) identify the breakpoints of interchanged chromosomes among detected reciprocal translocation lines; (3) determine the interchanged chromosomes by observing chromosome configurations in F_1 plants of translocation lines produced by test crosses. To investigate the location of breakpoints and rearrangements of interchanged chromosomes, Giemsa banding methods were applied to the materials (Linde-Laursen 1984b; Georgiev et al. 1985).

Materials and methods

In order to detect lines with reciprocal translocations in a World Barley Collection preserved in the Barley Germplasm Center of Okayama University, 1,240 cultivated barley lines chosen randomly from different regions of the world, together with 120 lines of wild barley, *Hordeum spontaneum* C. Koch, were crossed with a Chinese line having the standard karyotype, Tayeh 1 (OUC 331).

When partial sterility was noticed in F_1 plants in the field, seed fertilities of the F_1 plants and their parents were determined by counting the numbers of spikelets and seeds set in the central rows of 30 and 20 spikes. F_1 plants of the same crosses were grown again in a greenhouse, and the chromosome configurations in PMCs at metaphase I (MI) were examined. The spikes of the hybrids were fixed in Carnoy's fluid (6 parts absolute ethanol: 3 parts chloroform: 1 part glacial acetic acid), and the PMCs were squashed.

For identifying the interchanged chromosomes, two test crosses were made: (1) diallel crosses among the reciprocal translocation lines detected and (2) crosses between the reciprocal translocation lines and a series of trisomics of *Hordeum spontaneum* var. *nigrum* produced by Tsuchiya (1964).

The position of the breakpoints and the rearrangements of the interchanged chromosomes were determined by the junior auther, using Giemsa C- and N-banding and $AgNO_3$ staining of the chromosomes. The techniques applied were those developed by Linde-Laursen (1975, 1984a, 1985) and Linde-Laursen et al. (1980).

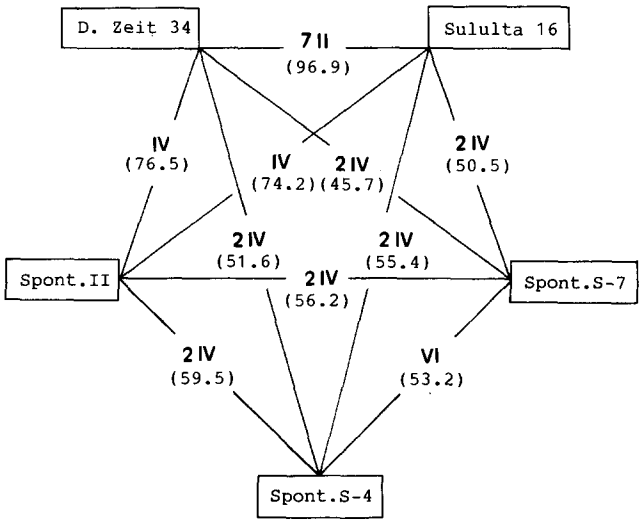

Fig. 1. Chromosome configurations and seed fertilities in F_1 plants between barley lines carrying different reciprocal translocations. ( ): Seed fertility in percent

Table 1. Number of lines of cultivated and wild barleys that produced fertile and partially sterile F_1 hybrids when crossed with Tayeh 1

Region	No. of lines tested		
	Fertile	Sterile	Total
Cultivated barley			
Japan	128		128
Korea	77		77
China	61		61
Nepal	139		139
India and Southwest Asia	403	1	404
Turkey	116		116
Europe	125	1	126
Ethiopia	139	51	190
Wild barley			
H. spontaneum	113	7	120

Results

Detection of spontaneous reciprocal translocation lines

In total, 1,240 lines of cultivated barley and 120 lines of wild barley were crossed with the tester, Tayeh 1, and the seed fertility of the F_1 plants was examined. F_1 plants from 60 of the 1,360 crosses showed partial sterility. Most of them were the F_1 plants of the tester crossed with cultivated Ethiopian lines and some wild barleys (Table 1). Their parents were normally fertile.

The chromosome configurations in PMCs of most of the partially sterile F_1 plants were normal, showing seven bivalents at MI and no lagging chromosome and/or chromosomal bridge at anaphase (AI). However, the F_1 plants of four cultivated Ethiopian lines (Addis Ababa 50, Debre Zeit 34, Debre Zeit 44 and Sululta 16) and three wild barley lines (Spont.II, Spont.S-4 and Spont.S-7) crossed with Tayeh 1 had one quadrivalent and five bivalents, indicating that these lines had a single reciprocal translocation. The seed fertilities of the F_1 plants and their parents are shown in Table 2. No spikes of the F_1 translocation heterozygotes were completely fertile. Individual seed fertilities ranged from 55.6% to 95.2% in six of the crosses, with the average seed fertility of 76.3%. F_1 plants of the seventh cross, Debre Zeit 44×Tayeh 1, averaged 59.1% in fertility. The seed fertilities of all parents were mostly complete.

Table 2. Seed fertility in central rows of spikes in seven translocation lines and their F_1 plants crossed with Tayeh 1

Okayama University access. no.	Translocation lines/tester	(Origin)	Seed fertility (%)			
			Parent		F_1	
			Mean	(Range)	Mean	(Range)
Translocation lines						
OUE 548	Addis Ababa 50	(Ethiopia)	98.3	(90.0–100)	74.6	(58.0–92.0)
OUE 227	Debre Zeit 34	(Ethiopia)	96.7	(86.7–100)	70.9	(57.1–90.5)
OUE 530	Debre Zeit 44	(Ethiopia)	98.8	(90.5–100)	59.1	(46.0–75.9)
OUE 259	Sululta 16	(Ethiopia)	97.1	(77.8–100)	75.0	(55.6–88.9)
OUH 654	Spont. II	(U.S.S.R.)	98.0	(90.9–100)	81.0	(69.2–92.3)
OUH 694	Spont. S-4	(Iraq)	98.2	(90.9–100)	82.2	(63.6–95.2)
OUH 697	Spont. S-7	(Iraq)	97.5	(90.9–100)	74.1	(56.5–86.0)
Tester						
OUC 331	Tayeh 1	(China)	97.5	(92.0–100)		

Table 3. Chromosome configurations observed in F_1 hybrids between four reciprocal translocation lines and seven trisomics

Translocation line	Trisomics						
	1 Bush	2 Slender	3 Pale	4 Robust	5 Pseudo-normal	6 Purple	7 Semi-erect
Debre Zeit 34	[a]	1_V+5_{II}	[a]	1_V+5_{II}	[a]	[a]	[a]
Spont. II	[a]	1_V+5_{II}	[a]	–	[a]	[a]	[a]
Spont. S-4	–	[a]	1_V+5_{II}	–	[a]	[a]	1_V+5_{II}
Spont. S-7	[a]	[a]	1_V+5_{II}	[a]	[a]	1_V+5_{II}	[a]

[a] $1_{IV}+1_{III}+4_{II}$

Identification of interchanges among the translocation lines

Chromosome configurations and seed fertilities of the F_1 plants derived from diallel crosses among two cultivated Ethiopian lines (Debre Zeit 34 and Sululta 16) and three wild barley lines (Spont.II, Spont.S-4 and Spont.S-7) are indicated in Fig. 1. As the chromosome configuration of the F_1 plants between Debre Zeit 34 and Sululta 16 was normal 7_{II} and their seed fertility was as high as that of the parents, these Ethiopian lines carry the same reciprocal translocation. Two other Ethiopian lines, Addis Ababa 50 and Debre Zeit 44, also have the same reciprocal translocation as the above two lines (data not shown).

The hybrids between these Ethiopian lines and Spont.II formed $1_{IV}+5_{II}$ at MI, indicating that the same two chromosomes are involved in the interchanges which occurred between the different arms.

The translocations in Spont.S-4 and Spont.S-7 are different from those of the Ethiopian lines and Spont.II, as the observation of the chromosome configuration $2_{IV}+3_{II}$ was observed in the hybrids between the two lines and the other translocation lines. The chromosome configuration in the hybrids between Spont.S-4 and Spont.S-7 was $1_{VI}+4_{II}$, indicating that their translocations involved one chromosome in common. The other translocated chromosomes in Spont.S-4 and Spont.S-7 are identified as chromosome 6 or 7, because a multivalent observed at diakinesis of all hybrids between either of the two lines and the other lines, including Turkey 193 (another cultivar of the standard karyotype), always attach to a nucleolus.

The seed fertility of the hybrids was, as expected, negatively correlated with the number of multivalents in MI. The average seed fertility was 97% in the hybrids with 7_{II}, 75% with $1_{IV}+5_{II}$, 53% with $2_{IV}+3_{II}$, and 53% with $1_{VI}+4_{II}$.

Determination of the chromosomes involved in the interchanges

Chromosome configurations were observed in the trisomic F_1 plants between four lines with different reciprocal translocations (Debre Zeit 34, Spont.II, Spont.S-4 and Spont.S-7) and a series of trisomics for chromosomes 1 to 7 (Table 3). Chromosome configuration of 1_V+5_{II} was observed in the F_1 plants of

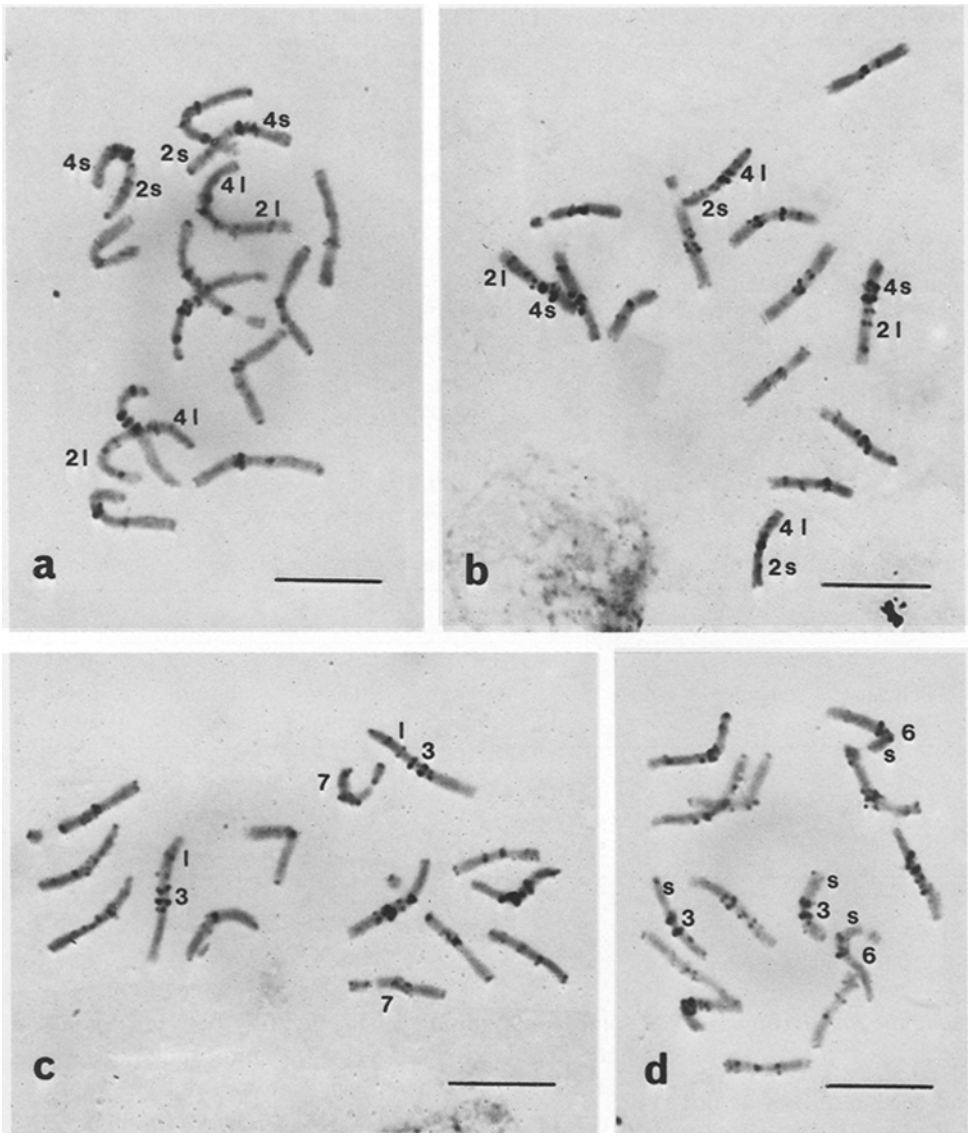

Fig. 2a–d. Giemsa C-banded somatic metaphase chromosomes of four lines carrying spontaneous reciprocal translocations: **a** Debre Zeit 34; **b** Spont. II; **c** Spont. S-4; **d** Spont. S-7. *Figures* refer to chromosome numbers and *letters* to unmodified arms. s = short arm, l = long arm, Bar = 10 μm

two cross combinations between the series of trisomics and each of the translocation lines except for Spont.II, which only showed 1_V+5_{II} when crossed with the trisomic for chromosome 2. The other F_1 hybrids showed $1_{IV}+1_{III}+4_{II}$. These results indicate that the interchanged chromosomes of Debre Zeit 34, Spont.S-4 and Spont.S-7 are chromosomes 2 and 4, 3 and 7, and 3 and 6, respectively. In Spont.II one of the interchanged chromosomes is chromosome 2, and the other one is assumed to be chromosome 4, because chromosome configuration of $1_{IV}+1_{III}+4_{II}$ was observed invariably in F_1 plants between Spont.II and trisomics for chromosomes 1, 3, 5, 6, and 7.

Localization of breakpoints and rearrangements of chromosomes

The comparison of chromosome morphology and Giemsa C-banding patterns of the translocation lines with those of a standard karyotype revealed the position of breakpoints in the interchanged chromosomes of Debre Zeit 34, Spont.II, Spont.S-4, and Spont.S-7 (Figs. 2 and 3). Debre Zeit 34 has the breakpoints at the centromeres of chromosomes 2 and 4, which are same as Debre Zeit 44, Addis Ababa 50 and Sululta 16. All four lines have the translocated chromosomes, 2S+4S and 2L+4L (Figs. 2a and 3a). However, Debre Zeit 34 differs from the other Ethiopian lines in the banding pattern of chromosome 7. The new banding variant found in Debre Zeit 34 is named 7G, whereas chromosome 7 of the other three Ethiopian lines correspond to the banding variant 7E (Linde-Laursen 1981). Furthermore, Debre Zeit 34 shows new banding variants designed 2H and 6J.

The breakpoints in Spont.II are also at the centromeres of chromosomes 2 and 4 like in the above-mentioned Ethiopian lines, but the arm combinations

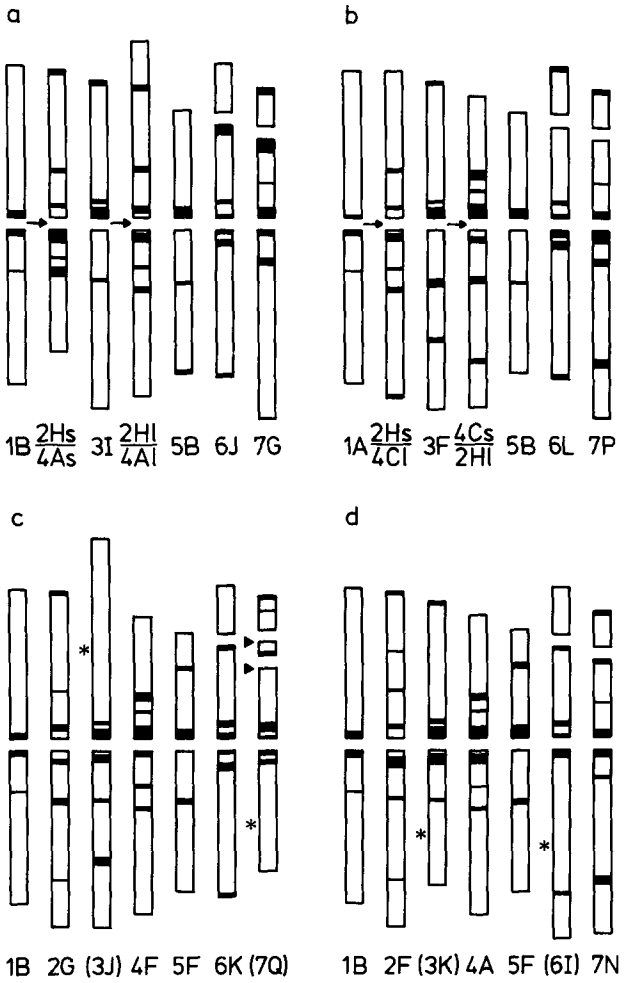

Fig. 3a–d. Idiograms of the chromosomes of four lines carrying spontaneous reciprocal translocations. Relative sizes and positions of C-bands are indicated by *solid bands*. **a** Debre Zeit 34; **b** Spont. II; **c** Spont. S-4; **d** Spont. S-7. *Arrows* and *asterisks* indicate exact and approximate positions of breakpoints, respectively. *Arrowheads* point to approximate positions of breakpoints of a paracentric inversion. *Figure-cum-capital letters* designate the banding pattern variants after Linde-Laursen (1981). The designation of translocated chromosome segments are given *in parentheses*. *s* and *l* in **a** and **b** refer to short and long chromosome arm, respectively

Table 4. Length of satellites and arms of chromosome 7 in Spont. S-4 and Turkey 193 (average of five mitotic metaphase plates of their F_1 hybrids)

Parent	Average length ± SD (μm)			
	Satellite	Short arm	Long arm	Total
Spont. S-4	2.3±0.33	2.1±0.39	4.5±0.25	9.0±0.93
Turkey 193	1.4±0.24	2.8±0.29	6.7±0.72	11.0±1.13

of the interchanged chromosomes are different, namely, 2S+4L and 4S+2L (Figs. 2b and 3b). A unique feature of the banding patterns of Spont.II is the absence of C-bands at the nucleolar constrictions of chromosomes 6 and 7. The banding variants of Spont.II are designated 6L and 7P.

The breakpoints in Spont.S-4 are in the short arm of chromosome 3 and the long arm of chromosome 7. A reconstructed chromosome 3 has the long arm carrying a translocated segment longer than the standard long arm, and a reconstructed chromosome 7 has the long arm shorter than that of the standard karyotype (Figs. 2c and 3c; Table 4). New banding patterns are observed in chromosomes 3, 4, 6 and 7 of Spont.S-4. These variants are named 3J, 4F, 6K and 7Q.

In Spont.S-7 the breakpoints are in the long arms of chromosomes 3 and 6. Compared with the standard karyotype, Spont.S-7 is characterized by a reconstructed metacentric chromosome 3 and a reconstructed chromosome 6 with the long arm similar in length to that of chromosome 7 (Figs. 2d and 3d). A new banding variant of chromosome 3 found in Spont.S-7 is named 3K. In Spont.S-4 and Spont.S-7 the precise locations of the breakpoints in the interchanged chromosomes cannot be determined by C-banding since the breakpoints are distal and there are no conspicuous C-band markers near the breakpoints.

Inversion found in chromosome 7 of Spont.S-4

The observation on the mitotic metaphase chromosomes in five cells of the F_1 hybrid between Spont.S-4 and Turkey 193 revealed that chromosome 7 of Spont.S-4 has a significantly larger satellite than that of Turkey 193 with the standard karyotype, and that a new constriction was observed in the satellite of chromosome 7 at one-third of its length from a larger, more proximal constriction in unstained, Feulgen-stained, C-banded or N-banded metaphase cells of Spont.S-4 (Figs. 3c and 4). However, total length of the satellite and short arm of chromosome 7 is the same between Spont.S-4 and Turkey 193 (Figs. 2c and 3c; Table 4). The satellite of chromosome 7 in Spont.S-4 is further characterized by a C-band at the larger constriction (Figs. 2c, 3c and 4), instead of the conspicuous band at the nucleolar constriction in the short arm of the normal chromosome 7 (Figs. 2 and 3; Linde-Laursen 1981). In contrast to the other C-bands, the nucleolar band in the satellite is not stained by N-banding, indicating that its chromatin is similar to that of a band found in the short arm of a normal chromosome 7 (Linde-Laursen 1981).

The morphology and banding pattern of the satellite suggested that the aberrant chromosome 7 of

Table 5. Characteristics of the Ethiopian barley lines carrying spontaneous reciprocal translocations

Okayama University access. no.	Line	Reaction to powdery mildew races[a]			Alleles at esterase isozyme loci		
		I	IV	IX	*Est-1*	*Est-2*	*Est-4*
OUE 548	Addis Ababa 50	R	R	M	*Pr*	*Fr*	*Su*
OUE 227	Debre Zeit 34	R	R	R	*Al*	*Fr*	*At*
OUE 530	Debre Zeit 44	R	R	M	*Al*	*Fr*	*At*
OUE 259	Sululta 16	R	R	S	*Al*	*Fr*	*At*

[a] R = resistant; M = moderately resistant; S = susceptible

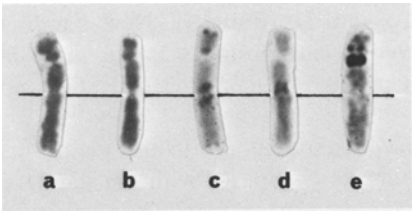

Fig. 4. *a–e* Chromosome 7 in mitotic metaphase of a *H. spontaneum* line, Spont. S-7. *a* unstained; *b* Feulgen-stained; *c* Giemsa C-banded; *d* N-banded; *e* stained with silver nitrate

Spont.S-4 carries a paracentric inversion produced between two breaks, one at a distal position in the short arm and the other in the nucleolus organizer region (NOR), having two tandemly arranged NORs. This conformation is verified by two darkly stained bands at the sites of the two constrictions with silver nitrate, the proximal one being thicker than the distal one (Fig. 4) (Linde-Laursen 1984a). Although an interphase cell of this line might be expected to have a maximum of six nucleoli, i.e., four from chromosome 7 and two from chromosome 6, there was no cell with more than four nucleoli and micronucleoli, suggesting that the new constriction in the satellite of chromosome 7 was not active as a NOR.

The inversion in Spont.S-4 is not proved by observing the meiotic cells of F_1 plants between Spont.S-4 and Turkey 193. Eight of 162 anaphase I (AI) and telophase I (TI) cells formed bridges, with no cell having a fragment. In the second meiotic division, a few cells formed fragments at metaphase II (MII), anaphase II (AII), or telophase II (TII). Two cells had a bridge, but only one cell had both a fragment and a bridge.

Discussion

In the present investigation, the four reciprocal translocation lines of cultivated barley were found among lines collected in a restricted area around Addis Ababa, the capital of Ethiopia. They are characterized by a 6-rowed (irregulare) ear, covered and blue kernel, and short rachilla hair, and have the same breakpoints on chromosomes 2 and 4, suggesting that their rearranged chromosomes are of common origin. They show slight differences in C-banding patterns, reaction to Japanese mildew races, and alleles at esterase isozyme loci (Table 5). These facts do not contradict the above suggestion.

In a wild relative of cultivated barley, *Hordeum spontaneum* C. Koch, three lines were found to have reciprocal translocations, which seem to have occurred independently of each other. One of the lines was collected in Turkmenia, U.S.S.R., and two others at different places near Sulaymaniyah in the northeastern part of Iraq, less than 40 km apart from each other. Three chromosomal rearrangements (two reciprocal translocations and one inversion) were detected in 39 lines of *H. spontaneum* var. *spontaneum,* whereas no chromosomal rearrangement was observed in 30 lines of *H. spontaneum* var. *proskowetzii* and 26 lines of cultivated barley collected in Iraq by Prof. S. Sakamoto, Kyoto University, in 1970. These facts may suggest that *H. spont.* var. *spont.* is more variable than two other taxa, and that the present translocations have occurred recently or that outcrossing is rare in this species.

Spont.S-4 has two chromosome rearrangements, namely, a reciprocal translocation and an inversion. Linde-Laursen (1983) found a similar combination of chromosomal rearrangements in the barley translocation line T1-6i, which was induced by neutron irradiation. The rearrangements in the latter line were probably induced simultaneously through neutron irradiation (Ramage 1971), whereas the spontaneous rearrangements in Spont.S-4 may have occurred independently of each other. As in T1-6i, the presence of the paracentric inversion in Spont.S-4 does not form bridges-cum-fragments at AI in its heterozygotes. The reason might be that the breakpoints of both inversions were proximal enough to leave terminal nonrearranged chromosome segments sufficiently large for a normal formation of the distally localized chiasmata (Linde-Laursen 1982).

Finally, the application of Giemsa C- and N-banding techniques to the present material was useful in identifying the chromosome parts involved in rearrangements. These techniques have an advantage over the conventional test crosses for the identification of translocated chromosomes and their breakpoints by saving time and labor, as mentioned by Linde-Laursen (1984b) and Georgiev et al. (1985).

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