Theor Appl Genet (1984) 68:433–439

Acrotrisomic analysis in linkage mapping in barley (*Hordeum vulgare* L.)*

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Received January 29, 1984; Accepted February 28, 1984
Communicated by Å. Gustafsson

Summary. Three acrotrisomic lines, Triplo IL^{1S}, $3L^{3S}$, and $4L^{4S}$, each carrying an extra acrocentric chromosome, were used for cytogenetic linkage mapping of barley chromosomes. The cytological structures of the acrocentric chromosome of the three acrotrisomic lines were studied with an improved Giemsa N-banding technique. The long (1L) and short arm (1S) of chromosome 1 had deficiencies of approximately 38% and 65%, respectively. The percentages of deficiencies were 0 and 77.8% for 3L and 3S, and 31.7 and 59.3% for 4L and 4S, respectively. All three genes tested (*br*, f_c, *gs3*) in 1S and all three genes tested, *f8*, *n* and *1k2* in 1L showed a disomic ratio indicating that they are located in the deficient segments. Two genes (a_c, *yst2*) located in the middle segment of 3S in linkage map showed a trisomic ratio, and two others a_n, x_s showed a disomic ratio. The only gene (*f9*) tested in 4L showed a trisomic ratio. Two genes (*lg4*, *gl*) located in the proximal segment of 4S in the linkage map showed a trisomic ratio, whereas two genes (*br2*, *gl3*) located distally in 4S showed a disomic ratio, indicating that the breakage occurred between *gl* and *br2*. This experiment demonstrates a new method for physical localization of genes on chromosome segments in material such as barley in which pachytene analysis can not be effectively used for accurate determination of break points in structural changes. Problems associated with this new technique are discussed.

Key words: Acrotrisomic, Acrocentric chromosomes – Cytogenetic linkage mapping – Barley – Deficiency

* Contribution from the Department of Agronomy and published with the approval of the Director of Colorado State University Experiment Station as Scientific Series Paper No. 2823. Supported by USDA/SEA Competitive Research Grant Nos. 5901-0410-9-0334-0 and 82-CRCR-1-1020 and USDA-CSU Cooperative Research Grant 58-9AHZ-2-265

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Introduction

Linkage maps of barley were first developed by conventional genetic analysis (Robertson 1939; Robertson et al. 1941; Smith 1951). It was then considered that all seven possible linkage groups corresponding to the haploid number of seven chromosomes in diploid barley, *Hordeum vulgare* (2n = 2x = 14), were established. With the introduction of cytogenetic methods, such as translocation analysis and trisomic analysis, all seven linkage groups were cytogenetically established in barley, and the concerted system for chromosomes, linkage groups, key marker genes and trisomic types was established (Kramer and Blander 1961; Tsuchiya 1961) as shown in Table 1.

The next contribution of cytogenetic methods to linkage mapping was the association of chromosome arms with marker genes and the localization of the centromere position in the linkage maps by means of telotrisomic analysis (Fedak et al. 1972; Tsuchiya 1972a, b, 1983; Tsuchiya and Singh 1982). Telotrisomic analysis also resulted in reversion of the linkage map of chromosome 5, in that the long- and short-arm relation was reversed from the previously established map (Tsuchiya 1972b). The final revision in linkage maps was made after Giemsa banding techniques (Linde-Laursen 1975; Noda and Kasha 1978; Singh and Tsuchiya 1982a, b) were applied to identify the extra telocentric chromosomes in telotrisomic plants. A new approach of combining acetocarmine and Giemsa staining techniques (Singh and Tsuchiya 1982a) provided conclusive evidence that two telocentric chromosomes previously designated 3S (short arm of chromosome 3) and 4S were actually the long arm of the respective chromosomes, 3L and 4L (Singh and Tsuchiya 1982b). This designation corresponds with the expression of morphological characteristics of those telotrisomic plants (Tsuchiya 1971a, 1972c; Singh and Tsuchiya 1977). The most recent designation of chromosome arms in relation to marker genes and linkage maps is presented by Singh and Tsuchiya (1982b).

The next step in linkage mapping is the physical localization of genes in the chromosome maps. However, it has been difficult to use such structural changes

Table 1. Interrelationships between trisomics, chromosomes, and key marker genes in the respective linkage groups of barley

Trisomic type	New linkage group and chromosome numerals	Key marker gene pair	Previous designations	
			Chromosome	Linkage group
Triplo 1 (Bush)	1	*Nn*	b	III, VII
Triplo 2 (Slender)	2	*Vv*	f	I
Triplo 3 (Pale)	3	*Uzuz*	c	VI
Triplo 4 (Robust)	4	*Kk*	e	IV
Triplo 5 (Pseudo-normal)	5	*Bb*	a	II
Triplo 6 (Purple)	6	*Oo*	g	new
Triplo 7 (Semi-erect)	7	*Rr*	d	V

as translocation stocks for this purpose because accurate determination of the break points is extremely difficult without pachytene analysis. Barley is not suitable for pachytene chromosome analysis.

Trisomic plants with extra acrocentric chromosomes – designated acrotrisomics – are the only available material for the physical localization of genes in chromosome maps in barley at present. In this article, the authors report the principle of acrotrisomic analysis and some results, together with discussion of some advantages and problems in acrotrisomic analysis.

Materials and methods

Materials used were three acrotrisomic lines obtained in the progenies of primary trisomics or triploids (Table 2). They were all grown in the greenhouse for morphological study, cytological analysis and genetic tests.

Chromosomes were studied in parental trisomics, F_1 hybrids and all plants in F_2 populations to eliminate possible abnormal plants carrying chromosome complements other than the original acrotrisomic type and disomic plants. Extra acrocentric chromosomes were identified by the combination of acetocarmine and Giemsa staining for the same cells (Singh and Tsuchiya 1982a) and/or by morphological similarities to the primary trisomic types in barley (Tsuchiya 1967). Three acrocentric chromosomes were designated acro $1L^{1S}$, $3L^{3S}$, and $4L^{4S}$, and the acrotrisomic plants were designated Triplo $1L^{1S}$, Triplo $3L^{3S}$, and Triplo $4L^{4S}$, respectively.

Acrotrisomic plants as female parents were crossed with multiple genetic marker stocks and some single genetic marker stocks. Table 3 gives a list of the genetic stocks used in this experiment. F_1 hybrids were separated into two groups, acrotrisomics and diploids. All acrotrisomic F_1 plants and 2 to 3 diploid F_1 plants were transplanted into 15-cm pots. Some 150 to 200 F_2 seeds from acrotrisomic F_1's were germinated in germinating boxes, roots collected from individual plants pretreated in ice water (± 1 °C) for 15–20 h and directly transferred into 0.8% acetocarmine. The modified squash preparation technique was used for chromosome studies (Tsuchiya 1971b). Plants were transplanted into peat pots in wooden flats to study genetic segregation ratios.

The theoretical segregation ratios in acrotrisomic analysis are the same as those for telotrisomic analysis worked out by Reeves et al. (1968) and shown diagrammatically in Fig. 1.

Since chromosome numbers of all F_2 plants were counted, the genetic segregation ratio was calculated separately for disomic and acrotrisomic portions.

Table 2. Acrotrisomic plants and their origin

Acrotrisomic type	Origin	Authority
$1L^{1S}$	Telotrisomic 1S	Tsuchiya 1979
$3L^{3S}$	Triploid hybrid (OAC21 4x × Montcalm 2x)	Tsuchiya 1971b
$4L^{4S}$	Primary trisomic 4 (Robust)	Tsuchiya 1971b

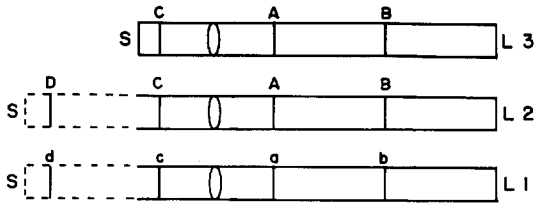
Table 3. List of genes used in this experiment

Gene symbol	Phenotype	Chromosomal location
br	brachytic	1S
f_c	chlorina	1S
gs 3	glossy sheath 3	1S
f8	chlorina 8	1L
n	naked (hulless) karyopsis	1L
lk 2	short awn 2	1L
x_s	xantha	3S
a_n	albino	3S
yst 2	yellow streak 2	3S
a_c	albino	3S
gl 3 (= gl 4)	glossy seedling 3	4S
br 2	brachytic 2	4S
gl (= gl 2)	glossy seedling	4S
lg 4	light green 4	4S
f9	chlorina 9	4L

Results

Cytological identification of acrocentric chromosomes

The acrocentric chromosomes were at first tentatively identified by their origin from the primary or telosomic



	D·d	C·c	A·a	B·b
2x	3·1	3·1 (25%)	3·1 (25%)	238·50 (17.4%) or 4.76·1
2x + Iacro	3·1	all (4)·0	all (4)·0	283·5 (1.74%) or 56.6·1
Total	3·1	7·1	7·1	521·55 (9.55%) or 9.47·1

Fig. 1. Summary of the expected segregation ratios in the F_2 generation from the acrotrisomic F_1 hybrid. This ratio is dependent on random chromosome and random chromatid segregation with a 50% expected female transmission rate of the extra acrocentric chromosome. The acrocentric chromosome (*3*) carries the dominant gene *C* in the short arm, and one of the normal chromosomes (*2*) carries the two dominant genes *C* and *D* in the complete short arm. Both chromosomes came from the female parent and also carry dominant genes *A* and *B* in their long arms. One normal chromosome (*1*) came from the male parent carries the four recessive genes *a, b, c* and *d*. The genes *Aa* and *Cc* are located near the centromere, genes *Bb* and *Dd* far from the centromere. *AAa* and *CCc* – Random chromosome segregation; *BBb* – Random chromatid segregation; *Dd* – Disomic segregation

trisomics and/or the morphological similarities of the acrotrisomic plants to the primary trisomics. Combined techniques of acetocarmine-Giemsa staining (Singh and Tsuchiya 1982 a) provided conclusive evidence to support the preliminary identification by their origin and/or plant morphology. The somatic karyotypes of three acrotrisomic types are shown in Figs. 2–4. The Giemsa-stained acrocentric chromosome and its homologous normal chromosomes are shown in Fig. 5.

Acrocentric chromosome $1L^{1S}$. The total chromosome length was much shorter than the normal chromosome 1. The Giemsa banding technique in combination with acetocarmine staining, as originally proposed by Nakata et al. (1977), showed that the long arm of chromosome 1 (1L) has a dark centromeric band and the short arm (1S) has a dark centromeric band and two less dark intercalary bands (Singh and Tsuchiya 1982 a, b). The acrocentric chromosome $1L^{1S}$ shows only one lightly stained band in the short arm (Fig. 5 a), indicating that deficiencies occurred not only in the distal but also in the proximal segments of both the long and the short arm. The centromere seems to be intact (Figs. 2 and 5 a).

Acrocentric chromosome $3L^{3S}$. Chromosome measurement showed that 3L was intact with no deficiency. However, 3S apparently had a 77.8% deficiency (Figs. 3 and 5 b). Since the proximal band in the short arm is approximately 33% of 3S (Singh and Tsuchiya 1982 a, b), and the remaining 22% of 3S appears to be band material, the breakage probably occurred in the proximal band.

Acrotrisomic $4L^{4S}$. Chromosome 4 is the most heavily Giemsa-banded chromosome, with some 50% of the entire chromosome banded. Measurements indicated that 4L and 4S had deficiencies of 31.7% and 59.3%, respectively. Giemsa staining suggested that proximal heterochromatic bands were intact and distal segments were deficient in both arms (Figs. 4 and 5 c).

Morphological characteristics of acrotrisomic plants

Morphological characteristics were useful for preliminary identification of the acrotrisomic plants.

Acrotrisomic $1L^{1S}$. Gross morphological features of Triplo $1L^{1S}$ are very similar to those of the primary trisomic and the telotrisomic for the long arm of chromosome 1 (1L), with narrow and dark green leaves, many tillers, rather small spikes, long awns, and narrow seeds. Some leaves are fused at the margin resulted in onion-like leaves.

Acrotrisomic $3L^{3S}$. Morphological characteristics of this acrotrisomic are similar to primary trisomic 3 (Triplo 3) and to the telotrisomic for 3L (Triplo 3L). Plants have pale green color in general; revoluted leaves with tip extremely twisted; prominent hairs on the surface of leaf blades, especially of the third and fourth leaves; compact spikes; slightly shorter awns; and high sterility.

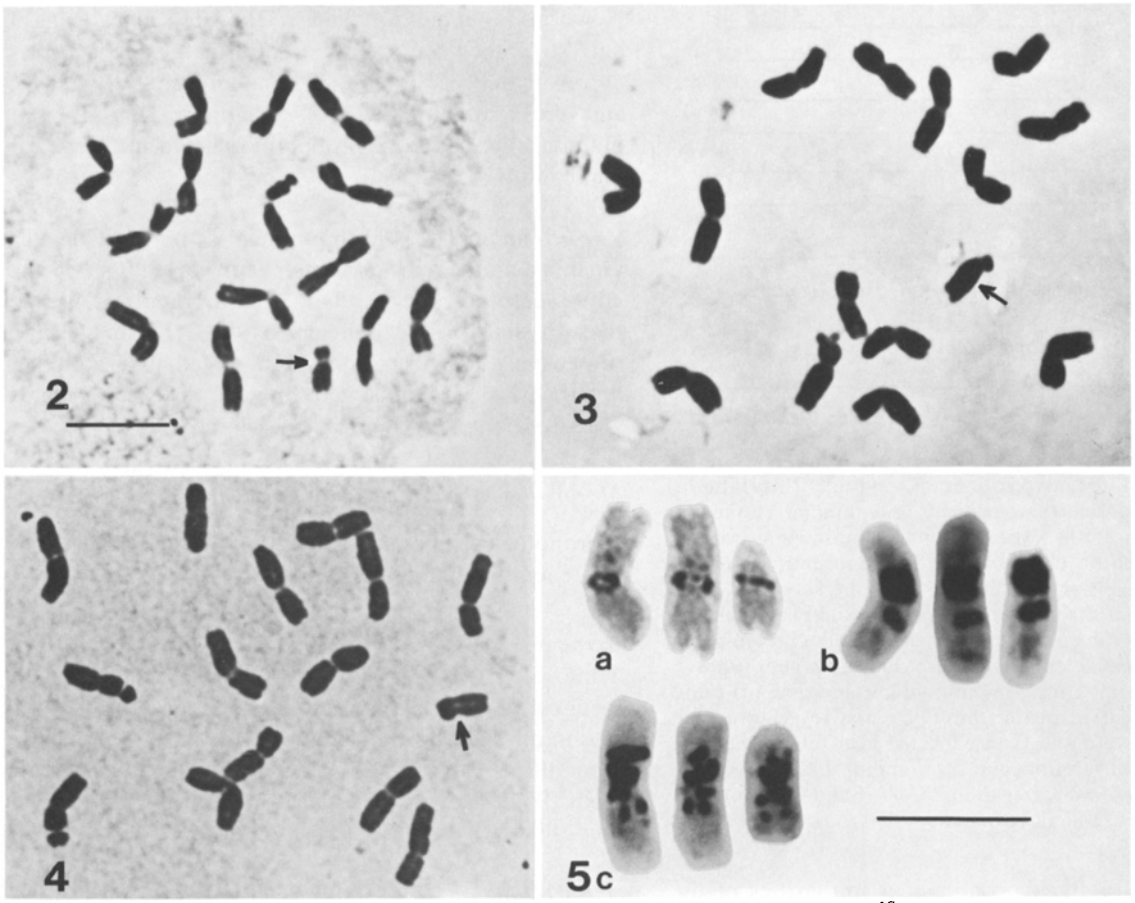
Acrotrisomic $4L^{4S}$. The acrotrisomic plant for $4L^{4S}$ was so similar to its parental trisomic, Triplo 4 or Robust, that it was impossible to distinguish the two types by morphological characteristics. The two types were distinguished only by karyotype analysis. Both have short and thick culms; slightly shorter, dark green and revoluted leaves; and short, compact spikes.

Genetic analysis

Acrotrisomic $1L^{1S}$. Three Mendelian recessive mutant genes for the short arm and three recessive genes in the long arm of chromosome 1 were analyzed, with the results shown in Table 4.

Three genes, *br*, f_c, and *gs3*, showed disomic ratios (Table 4), indicating that they are located in the missing distal segment of chromosome 1S.

Similarly, all three genes (*f8, n, lk2*) located in 1L showed a disomic ratios, indicating that they are on the deficient segment of 1L.



Figs. 2–5. Somatic chromosomes in three acrotrisomic types. **2** Karyotype of Triplo $1L^{1S}$. **3** Karyotype of Triplo $3L^{3S}$. **4** Karyotype of Triplo $4L^{4S}$. **5** Giemsa banded trisomes for Triplo $1L^{1S}$(a), $3L^{3S}$(b) and $4L^{4S}$(c). Figs. 2–4 ×1,360; Fig. 5 ×2,040

Table 4. Genetic segregation ratios in F_2 populations of crosses between acrotrisomic lines and various genetic stocks

Genes Tested		2x			2x+1			Total		
		+	a*	Total	+	a*	Total	+	a*	Total
$1L^{1S}$× *br*	(1S)	79	26	105	33	8	41	112	34	146
fc	(1S)	77	28	105	31	10	41	108	38	146
gs3	(1S)	79	26	105	31	10	41	110	36	146
f8	(1L)	48	19	67	41	9	50	89	28	117
lk2	(1L)	56	15	71	44	5	49	100	20	120
n	(1L)	95	18	113	67	5	72	162	23	185
$3L^{3S}$× a_c	(3S)	45	14	59	32	0	32	78	14	92
yst2	(3S)	84	12	96	34	0	34	121	12	133
a_n	(3S)	49	17	66	32	9	41	81	26	107
x_s	(3S)	59	15	74	30	12	42	89	27	116
$4L^{4S}$× *lg4*	(4S)	64	20	84	28	0	28	92	20	112
br2	(4S)	97	32	129	37	9	46	134	41	175
gl	(4S)	110	19	129	46	0	46	156	19	175
gl3	(4S)	80	31	111	31	6	37	111	37	148
f9	(4L)	90	16	106	62	0	62	152	16	168

* All recessive genes were designated *a* in this table

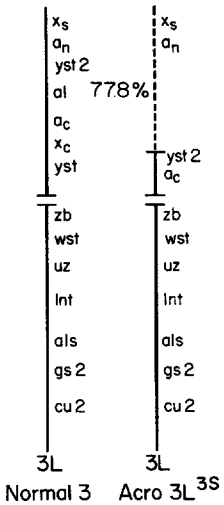


Fig. 6. The linkage map of chromosome *3*. *Left* Normal map (Tsuchiya 1981). *Right* Map for acrocentric chromosome $3L^{3S}$. Note the breakage occurred between a_n and *yst2*

Acrotrisomic $3L^{3S}$. Since the long arm has no deficiency, genetic analysis was conducted with genes located on the short arm (3S) only. Two genes tested (a_c, *yst2*) are located within the proximal 36.4% of the short arm in the genetic linkage map of chromosome 3 (Takahashi and Fukuyama 1977). The genetic data (Table 4) showed that a_c and *yst2* are located in the proximal segment consisting of 22.2% of the short arm of the acrocentric chromosome. Genes a_n and x_s showed a disomic ratio indicating that chromosome breakage occurred between a_n and *yst2* and the chromosome segment distal to *yst2* is deficient. Even though the results obtained are limited, it seems that genes located midway in the map are physically located within the proximal 22.2% segment of the short arm of chromosome 3 (Fig. 6).

Acrotrisomic $4L^{4S}$. As already mentioned, the acrocentric chromosome of this acrotrisomic plant has deficiencies in both arms; approximately 32% in the long arm and 60% in the short arm (Figs. 4 and 5c). One gene in the long arm (*f9*), and four genes (*1g4, br2, g13, g1*) in the short arm were analyzed genetically with the results shown in Table 4.

As expected, gene *f9* showed a trisomic ratio. Genes *1g4* and *g1* (=*g12*) in the short arm showed a trisomic ratio, while *br2* and *g13* showed a disomic ratio (Table 4). This result indicated that breakage occurred between *br2* and *g1* (=*g12*) in the map.

Discussion and conclusions

The ideal method of cytogenetic linkage mapping is that of salivary gland chromosomes in combination with various structural changes such as deficiencies and inversions in *Drosophila* (Roberts 1976), or pachytene analysis with deficiencies in maize (McClintock 1932; 1933; Rhoades 1955; Carlson 1977) and tomato (Khush and Rick 1968; Rick 1971; Khush 1973), and other chromosomal aberrations (Burnham 1962). These methods deal with the direct relationship between genes and specific chromosome segments. It is a prerequisite to have salivary gland or pachytene chromosomes available for these direct methods of cytogenetic linkage mapping. Unfortunately, barley chromosomes are not suitable for pachytene analysis (MacDonald 1961; Sarvella et al. 1958; Singh and Tsuchiya 1975). Therefore, it has been difficult in barley to use cytogenetic methods such as translocation analysis (Persson 1969a, b) or inversion analysis which need rather accurate information on the physical break points (Tsuchiya 1983). Acrotrisomic plants reported in this paper may provide an approach with which physical localization of genes (gene mapping) may be accomplished.

Although an acrotrisomic plant for $4L^{4S}$ was first isolated in 1964, acrotrisomic analysis was not possible until information on the arm location of genes and definite location of the centromere in the linkage map become available. Telotrisomic plants have been used in the last 10 years (Fedak et al. 1971, 1972; Tsuchiya 1971a, b, 1983; Tsuchiya and Singh 1982) since the first telotrisomic plant for 1L (Triplo 1L) and 1S (Triplo 1 S) were reported in barley (Tsuchiya 1969). The centromere positions were determined in linkage maps for the five nonsatellited chromosomes (chromosome 1 through 5) and some 50 genes were associated with 10 arms of those five nonsatellited chromosomes (Fedak et al. 1972; Tsuchiya 1971a, 1972a, b, 1981, 1982; Tsuchiya and Singh 1982).

Systematic acrotrisomic analysis started in 1977 with an acrotrisomic for $1L^{1S}$ with the results described in this article and others (Shahla 1980; Hang 1981; Tsuchiya and Fujigaki 1981).

A serious problem associated with this method is the uncertainty of the nature of breakage in the acrocentric chromosomes. The origin of acrocentric chromosomes is breakage in chromosome arm(s) and the healing of broken ends or fusion with another broken end. Since most of the barley chromosomes are metacentric or submetacentric, substantial deficiency of a segment in one arm results in an acrocentric chromosome. The mode of occurrence of a deficiency is basically one of the two types illustrated diagrammatically in Fig. 7. Figure 7A shows a simple terminal deficiency which needs only one break in the arm. Figure 7B is an intercalary segmental deficiency which needs at least two breaks in the arm.

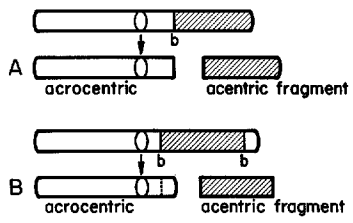


Fig. 7A, B. Diagrammatic illustration of the mode of origin of acrocentric chromosome. **A** Single break at *b* point resulting in acrocentric chromosome with healed broken end and acentric fragment. **B** Two breaks at *b* points with the result of an acrocentric chromosome with original telomere and acentric fragment

Deficiencies in both arms also results in an acrocentric chromosome provided the deficient segments in both arms are substantially different from each other. If the telomere concept of Muller (1940) is correct, all breakages should be considered to be at least two breaks with the original telomere intact. However, according to McClintock (1941), broken ends of meiotic chromosomes will heal when the chromosomes enter into sporophytic tissue. Since the acrocentric chromosomes used in this study have been obtained in the progeny of primary or telosomic trisomics or triploid plants, it is reasonable to assume that the simple breakage which occurred in the extra chromosome (Fig. 7 A) went through a breakage-fusion-bridge cycle and the broken end eventually healed as suggested by McClintock (1941). The short arm of acrocentric chromosome $3L^{3S}$ and both of long and short arms of acrocentric $4L^{4S}$ may belong to this type. Acro $1L^{1S}$ seems to have intercalary deficiencies resulted from multiple breaks and fusion of broken ends (Fig. 7 B) in both arms. The nature of brekage, single or double with an intercalary deficiency. may be studied by conventional genetic analysis using the back cross method with well-developed multiple genetic marker stocks. The Giemsa-banding technique will also provide more information on the nature of the breaks (Fig. 5).

The results so far obtained provide some information but also raise some questions. However, this experiment demonstrated a new method of cytogenetic linkage mapping in barley chromosomes. Application of this technique with the several additional trisomics now available that carry extra acrocentric or other fragment chromosomes with different break points will facilitate improvement of linkage maps of barley. This technique may be useful in other plant materials in which pachytene analysis is not possible.

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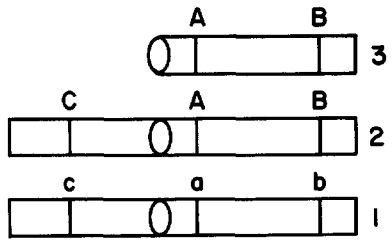
Erratum

Correction in the previous paper "Chromosome mapping in barley by means of telotrisomic analysis", T. Tsuchiya and R.J. Singh (Theor Appl Genet 61: 201–208, 1982).

In our paper published in this journal Tsuchiya and Singh presented a figure (Fig. 1) for the theoretical segregation ratios in telotrisomic analysis. All of the segregation ratios in the separate 2x and 2x+1 telo portion for all genes, *a, b,* and *c* were correct. However, in calculating a total of 2x and 2x+1 telo, the figures in 2x portion was supposed to be doubled for *B:b*. Since the 2x portion was not doubled, the segregation ratio for *B:b* in total was not correct. However, segregation ratios for *A:a* and *C:c* were correct, since both allele pairs segregate 3:1 ratio (except in the 2x+1 telo portion for *A:a*). Also the total figures were not changed for *A:a* and *C:c*. If the 'Total' figures were eliminated, the Fig. 1 could be used as it is. Actually, as shown in Tables 2 through 5, all segregation data were calculated separately for 2x and 2x+1 telo portion in Tsuchiya and Singh (1982), so that interpretation of the results presented in the previous paper (TAG 61: 201–208) was correct.

However, because of the problem in calculating *B:b* segregation in 'Total' figure, the authors would like to replace Fig. 1 (p. 203, TAG 61, 1982) by the one shown below. The segregation ratios shown in this "corrected Fig. 1" are the same as the ratios in Fig. 1 in this paper "Acrotrisomic analysis in linkage mapping in barley".



	C:c	A:a	B:b
2x	3:1	3:1(25 %)	238:50(17.4 %) or 4.76:1
2x + 1 telo	3:1	all(4):0 (0%)	283:5 (1.74 %) or 56.6:1
Total	3:1	7:1	521:55(9.55 %) or 9.47:1

Fig. 1