M. Feldman

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THE TELOCENTRIC CHROMOSOMES OF COMMON WHEAT[1]

E. R. SEARS[2] AND LOTTI M. S. SEARS[3]

Curtis Hall, University of Missouri, Columbia, Missouri, USA

ABSTRACT

The series of 42 telocentric derivatives of the wheat chromosomes has been completed. The telocentrics arose through misdivision of complete chromosomes, some in two steps by way of isochromosomes. All are in cv. Chinese Spring except 7DL, recently provided by E. R. Kerber, which is in 'Canthatch'. The two telos for each chromosome except 4A differ in length. All but eight of the ditelosomics, 1DS, 2AL, 2BS, 4Aβ, 4BS, 5AS, 5BS, and 5DS, are fertile. Double ditelosomics ($20'' + 2t''$) and double monotelosomics ($20'' + 2t'$) are maintained for all chromosomes except 7D, and dimonotelosomics ($20'' + t'' + t'$) for all telos except 7DS and 7DL. The principal uses of telocentrics are in providing cytologically recognizable chromosomes for identifying aneuploids, guarding against univalent shift, locating and mapping genes, determining chromosome morphology, transferring genes from alien chromosomes, and determining degrees of meiotic pairing and somatic association. Because the arm lengths of the chromosomes of group 4 and possibly group 2 do not correspond with homoeology, it is proposed that the arms should be redesignated according to homoeology, with p being used for short arms and q for long where there is no conflict with homoeology.

ORIGIN

All 21 chromosomes of common wheat (*Triticum aestivum*) have two arms, but the misdivision of univalents at meiosis gives rise to one-armed chromosomes, or telocentrics, and also to isochromosomes, which have two identical arms. All 42 telocentrics have now been obtained.

Eleven of the telocentrics (1AL, 2AS,4Aα, 5AL, 2BL, 3AS, 4BL, 1DL, 5DL, 6Ds, and 6DL) arose from isochromosomes, which had previously been produced by misdivision of ordinary chromosomes. One, 4Aα, involved three misdivisions ; first, of a normal 4A chromosome to form a telocentric; second, of the telocentric to yield an isochromosome; and third, of the isochromosome to produce again a telocentric.

The frequency with which misdivision occurs is relatively high for most chromosomes of 'Chinese Spring' wheat (E. Sears, 1952a, 1954; L. Sears, 1973; Morris *et al.*,

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[2]Geneticist, ARS, USDA, and Professor of Agronomy, University of Missouri.

[3]Assistant Professor of Agronomy, University of Missouri.

1977). Consequently, many of the telocentrics (or the isochromosomes from which they were derived) appeared among the progeny of selfed monosomics, without any special search being made for them. They occurred either in plants that superficially resembled nullisomics or in reasonably normal plants that were being routinely checked for monosomy preparatory to being used in crosses. Most or all of the telocentrics recovered as monosomes must have come from male gametes, for nullisomic pollen functions too rarely to allow much opportunity for female gametes carrying telocentrics to give rise to monosomic plants. For a male gamete carrying a telocentric to function other than rarely, the telocentric concerned must suffer little adverse selection in competition with the complete chromosome. Good examples of such telocentrics are those for the long arms of the chromosomes of group 5. These group-5 telos, however, were not recovered from selfed monosomics as often as certain others (E. Sears, 1954), because the plants monosomic for them were phenotypically similar to those monosomic for the complete chromosomes and were usually not examined cytologically. Monosomics for telo-6AS, on the other hand, closely resembled nullisomic 6A and as seedlings were often selected along with nullisomics for growing out and analyzing cytologically. Similar to 6AS in this respect were 2BL, 3BL, and 7BL (E. Sears, 1954).

Several telocentrics were discovered by observation of root-tip chromosomes of offspring of monosomics. Unfortunately, the presence of a telocentric in root-tip cells did not always insure its also being present at the flowering stage; in fact, nearly half failed to appear in PMC's. Presumably these were unstable telocentrics that could survive only a limited number of mitoses (see Steinitz-Sears, 1966).

Although the extensive data obtained concerning recovery of telo-5AL from mono-5A (E. Sears, 1952a) suggest that about 2% of the offspring of a monosomic should have a telocentric for a particular one of the two arms, certain telocentrics almost certainly do not appear in such high frequency (Table 1). In particular, repeated efforts to recover telo-7DL have been unsuccessful. Use of the marker *cn-D*1 (*chlorina*) on this arm made it possible to reduce the labor of assaying for the presence of the telocentric. Since mono-7D plants carrying *cn-D*1 are practically non-*chlorina,* their only fully *chlorina* offspring are those with two doses of the gene. This permits discarding the ca. 75% monosomics, which nearly always have a paternal, and therefore almost certainly complete, 7D. Among 1279 offspring of mono-7D carrying *cn-D*1, 356 were *chlorina*. Of these, 303 were examined cytologically, and nine proved to have one bivalent that included a telocentric chromosome. None of the five telocentrics tested, however, were from chromosome 7D. In contrast, in a similar experiment with chromosome 7A, 12 telocentrics were recovered among 1625 offspring of monosomics and all five tested were 7AL, the arm that carries *cn-A*1.

Although telocentrics for 7DS would not have been recovered in the foregoing experiment, root-tip analysis of more than 700 unselected offspring of mono-7D would have identified telo-7DS as well as -7DL. Two 7DS telocentrics were recovered.

On the assumption that female as well as male gametes carrying telo-7DL were being selected against, an experiment was devised in which this telocentric was expected

Table 1. The occurrence of particular telocentric chromosomes among the offspring of selfed monosomics

Telocentric concerned	No. offspring analyzed	No. with specified telocentric
1AS	140	1
1DS	370	1
2AL	130*	2
3AS	97	0
3BS	97	0
3DS	156	0
4BS	106	0
4DS	158	0
5BS	100	0
5DS	274	0
6AL	155	0
6DL	138	1**
7DL	2000*	0

*Approximate numbers.
**Actually an isochromosome from which the telocentric was subsequently derived.

to be favored over the complete 7D. In this material a pair of group-7 chromosomes from *Agropyron elongatum* (called 7Ag by E. Sears, 1972a) replaced one 7D chromosome. All gametes therefore had one 7Ag and some had 7D in addition. Male gametes carrying a telocentric 7D instead of the complete 7D were expected to function preferentially, because they had fewer duplicated genes. The 7D chromosome carried *cn-D*1, and the female parent was *cn*-D1 *cn*-D1. This permitted selection for offspring with two 7D chromosomes, including telocentrics for 7DL. However, in two experiments, involving a total of 456 offspring, no telocentrics were found, although 69 were identified that carried a complete 7D.

As noted earlier, 11 telocentrics were derived through misdivision of isomonosomes. In most cases the frequency of recovery of telocentrics from isochromosomes was reasonably high (Table 2, and Table 11 in E. Sears, 1954), but efforts to get telos 2AL and 5BS from the corresponding isochromosomes were unsuccessful. The rate of recovery of the telocentrics varied widely, being particularly high for 4BL and for 5BL (included in Table 2 although the 5BL telocentric presently maintained was not derived from an isochromosome). For the following isochromosomes that are either among the 11 parents of telocentrics or are included in Table 2, data are given in Table 11 of E. Sears (1954): 1AL(XIV), 2AS(IIR), 4Aα(IV), 5AL(IX), 2BL(XIIIR), 5BL(V), 6BS(XR), 1DL(XVII), 5DL(XVIII), and 6DS(XIX). The worst discrepancy between the two tables appears to be for 5BL; however, this difference can probably be accounted for by the fact that the cytologically analyzed plants in the 1954 table were a selected sample from a much larger population.

Table 2. Chromosome constitution of the progeny of certain isomonosomic plants, following selfing, or crossing as male

Arm concerned	Type of progeny	No. of offspring	Constitution for arm concerned and no. of plants				
			Iso	Telo	2 Isos	Iso + Telo	Nulli
2AS	crossed	17	8	1	0	0	8
2AL	selfed	40	40	0	0	0	0
4Aα	,,	16	9	0	0	1	6
4Aα	crossed	3	2	1	0	0	0
2BL	,,	36	33	1	0	0	2
4BL	selfed	9	4	3*	0	0	2
5BS	,,	48	26	0	2	0	20
5BL	,,	123	68	6	35	9	5
6BS	,,	135	87	1	36	1	10
6DL	,,	18	11	1	0	0	6

*Including 1 plant with 2 telos.

Designations

The first telocentric chromosomes to be maintained and distributed to other workers were ones that had been recovered in the early 1940's as monosomes in plants that were able to set selfed seed. For only two chromosomes, 3B and 4D, were both telocentrics obtained at that time; and because one 3B monotelo was partially asynaptic and one 4D poorly fertile, only one telocentric line of each chromosome was maintained. Eventually a complete set of 21 monotelosomics (or monoisosomics) was obtained, and these were given the symbol of the chromosome concerned, as III, XVII, etc. No distinction was made as to long or short; indeed, except for telos V(5B) and IX(5A), it was not yet known whether the telocentric represented the long or the short arm (E. Sears, 1954).

Eventually the remaining 21 telocentrics were sought and obtained. To distinguish between the two arms of the same chromosome, the word "long" or "short" was appended to the chromosome's symbol, if the relative lengths were known; otherwise, the telocentric already in existence was designated "right" and the new one "left." Since by this time (the middle 1960's) the Roman-numeral chromosome designations had been changed to the present ones, the telocentrics became known as 1AS(hort), 1AL, 4Ar(ight), 4A1(usually with the appended letter written as a sub- or superscript), etc. Until as late as 1968, however, the appended letter was often omitted if only one of the two telocentrics was involved and this was the one for the "right" (sometimes called "standard") arm.

In 1968 to avoid the ambiguity of using L for long and l for left, the Greek letter α was substituted for right and β for left (Kimber and Sears, 1968). Like r and l, α and β were used only for arms not yet identified as long or short, and as soon as a length

difference was detected, L and S were substituted. In order to help in properly identifying the telocentrics that have been distributed during a period of more than 30 years, each of the 21 telocentrics designated as α, r (or R) , or simply with a Roman numeral is specified in Table 3. These are the so-called "standard" telocentrics.

Table 3. The 42 telocentric chromosomes: their designations and their sources. The authors are deeply grateful to the various investigators who contributed to the completion of the series

Telocentric	Recovered by†	Telocentric	Recovered by†	Telocentric	Recovered by†
1AS	S. Lee-Chen	1BS	M. Muramatsu	1 DS	B. S. Panda
1AL*	M. Okamoto	1BL*		1DL*	
2AS*		2BS	‡	2DS*	
2AL		2BL*		2DL	Muramatsu
3AS	T. Miller	3BS		3DS	McIntosh
3AL*		3BL*		3DL*	
4Aα*		4BL*		4DS	P. Sallee
4Aβ	Okamoto	4BS	Muramatsu	4DL*	
5AS		5BS	Miller	5DS	McIntosh
5AL*		5BL*		5DL*	
6AS*		6BS*	Crosby-Longwell	6DS*	
6AL	R. A. McIntosh	6BL		6DL	
7AS	A. Crosby-Longwell	7BS	Crosby-Longwell	7DS*	
7AL*		7BL*	" "	7DL	E.R. Kerber

*A telocentric for the arm known at various times as "right", "alpha", or "standard."
†Those not credited to others were recovered by the senior author.
‡Recovered from the Cornell selection 82al–2–4–7, a derivative from a wheat-rye cross.

As a consequence of chromosomes 2A and 2B being assigned to the wrong genomes by Okamoto (1962), there was a period of a few years (1962-1966) when the 2A telocentric was maintained and distributed as 2B, and vice versa. Chapman and Riley (1966) corrected the error.

Six of the telocentrics, 2BS, 2DL, 4BS, 5DS, 6AL, and 7DL, first became available in material other than the standard variety, Chinese Spring. In order to have these telocentrics in the standard variety, crosses and backcrosses were made to Chinese Spring. There were 10 backcrosses of 2DL, five each of 2BS and 6AL, three of 4BS, and one of 5DS. Telo-7DL was only obtained near the end of 1976.

One telocentric, 5AS, is known to be not truly telocentric. We are indebted to P. Sallee for pointing out that this chromosome has a very short second arm. Telo-5DL was noted by Gill and Kimber (1974) to be deficient for a terminal segment.

Transmission

As previously noted, the telocentrics were first obtained either as monosomes or in the presence of the corresponding complete chromosomes. In both cases some data

on transmission (Tables 4,5) were usually obtained during the process of maintaining the line or deriving and maintaining the various derivative materials. To the data in Table 4 may be added those in Table 11 of E. Sears (1954) for telo-6AS (VI).

Table 4. Constitution of offspring of selfed plants monosomic for various telocentric chromosomes

Constitution	Chromosome arm and no. of plants of each constitution												
	1AS	1AL	2AS*	2AL*	3AS	3AL	4Aα	4Aβ	5AS	5AL	6AL	7AS	7AL
t″	5	5	5	11	1	4	13	1	1	3	1	1	0
t′	20	4	28	34	3	12	13	3	30	5	4	1	10
—	17	4	20	0	2	0	1	2	56	0	0	0	9
Total	42	13	53	45	6	16	27	6	87	8	5	2	19
	1BS	1BL		2BL	3BS	3BL	4BS	4BL	5BS	5BL	6BS	6BL	7BS
t″	0	1		1	3	26	0	8	1	9	—	1	3
t′	5	14		4	4	72	16	33	17	20	—	2	8
—	2	0		5	4	18	25	1	17	0	2	0	11
Total	7	15		10	11	116	41	42	35	29	16	3	22
	1DS	1DL	2DS		3DS	3DL	4DS	4DL	5DS	5DL	6DS	6DL*	7DS
t″	1	18	1		1	14	1	3	1	3	0	2	20
t′	41	32	10		5	35	3	10	3	7	47	6	57
—	83	0	5		1	3	0	4	6	0	9	12	0
Total	125	50	16		7	52	4	17	10	10	65	20	77

*Data mostly or all from 20″ + t's + i'L.

Table 5. Constitution of offspring of selfed plants with various monotelodisomes (20″ + t1″)

Constitution	Chromosome arm and no. plants of each constitution							
	1AS	2AS	4Aα	4Aβ	7AS	7AL	1DS	7DS
t″	0	2	8	2	1	8	0	0
t1″	2	4	—	15	31	—	5	1
1″	2	1	—	2	39	—	5	3
Total	4	7	149	19	71	138	20*	4

*Includes nine with 1′, one with il″.

On the assumption that female transmission for all the monotelosomes is 20–30%, the data suggest strongly that telocentrics 2AL, 3AL, 4Aα, 5AL, 1BL, 4BL, 5BL, 1DL, 5DL, and 7DS are transmitted through pollen in much the same way that the corresponding complete chromosomes are transmitted; that is, strongly selected for when

monosomic, and not selected against when the complete chromosome is also present. Telos 6AL, 7AS, 6BL, and 4DS may also be in this category, but additional data are needed.

Several telocentrics appear to have little advantage in male transmission over complete absence of the chromosome concerned: 5AS, 7AL, 4BS, 5BS, 7BS, 1DS, 5DS, and 6DL. Telos 1BS and 6BS may also belong in this category.

Telocentrics with an apparent intermediate rate of male transmission are 1AS, 1AL, 2AS, 4Aβ, 3BL, 3BS, 2DS, 4DL, 6DS, and possibly 3AS, 2BL, and 3DS.

As would be expected, when one telocentric has a high rate of male transmission, the telo for the other arm of the same chromosome has a low or at most intermediate rate of transmission. For chromosomes 1A, 3B, and probably others, both telos are transmitted at an intermediate rate.

Telocentric 1DS suffers not only from poor competitive ability in the monotelodisomic, but also from post-meiotic loss following relatively frequent pairing failure. In 100 microsporocytes of a 20″ + t″S + t″L plant, the short telocentrics were unpaired in 21 and the long telos in only 7 cells. Similar frequencies of pairing failure have been observed in 20″ + tl″S. The high frequency of 20″ + 1′ offspring of 20″ + tl″S in Table 5 must thus be due to pairing failure and frequent loss of both chromosomes. The loss is reflected in functioning nullisomic female gametes, whereas on the male side almost the only pollen that functions has a complete 1D.

Stability

In the only precise study of the stability of telocentric chromosomes in somatic tissue (Steinitz-Sears, 1966), no telocentric 3BS was as stable as the corresponding complete chromosome, and about 75% were too unstable to persist until the flowering stage. The most common aberration was simple loss of the telocentric, but evidently the telo occasionally underwent non-disjunction. There is evidence that a telocentric can also be converted into an isochromosome in somatic tissue (E. Sears, 1952b).

Although some degree of instability seems to be characteristic of telocentrics (see also E. Sears, *loc. cit.* and 1967), some are very nearly as stable as complete chromosomes, and a delicate test is necessary to demonstrate their instability. Most or all of the telocentrics for which seed stocks are maintained are believed to be of this type.

Fertility

Although none of the ditelosomics are of completely normal fertility, several have borne up to 200 seeds per plant (Table 6) under conditions such that the seed set on normal Chinese Spring was about 350 seeds. Only eight ditelos have always been fully sterile when selfed, and it is not unlikely that some of these would set if grown under ideal conditions. In particular, ditelo-1DS should be fertile, for occasional selfed

seeds are borne by nullisomic 1D. In homoeologous groups 3, 6, and 7 all the ditelosomics are fertile, whereas in group 5 none of the short-arm ditelosomics set selfed seeds. As pointed out by E. Sears (1954), it is female sterility that prevents seed setting in group-2 deficiencies and male sterility in the other groups.

Monotelosomics tend to be somewhat less fertile than the corresponding ditelosomics. Dimonotelosomics ($20'' + t'' + t'$) and monotelodisomics ($20'' + t1''$) show little or no reduction from normal in fertility.

The data in Table 6 are not all taken from plants grown in the same season under precisely the same conditions. Indeed, even this would not insure fair comparisons, for conditions that were ideal for one line would not necessarily be ideal for another. It was thought that over a number of seasons, the environment would be favourable one or more times for each ditelocentric line, and that maximum seed set would therefore be the fairest comparison. Unfortunately, data were available for only one to 11 plants of each ditelosomic, grown in no more than four different seasons. Nevertheless, the values given are believed to represent reasonably fairly the differences among the various ditelosomics.

Table 6. Maximum number of seeds borne by ditelocentric plants. Control (euploid) plants produce about 350

1AS	1AL	2AS	2AL	3AS	3AL	4Aα	4Aβ	5AS	5AL	6AS	6AL	7AS	7AL
63	187	49	0	101	122	96	0	0	124	47	177	71	69
1BS	1BL	2BS	2BL	3BS	3BL	4BS	4BL	5BS	5BL	6BS	6BL	7BS	7BL
39	206	0	50	71	115	0	118	0	199	111	79	205	130
1DS*	1DL	2DS	2DL	3DS	3DL	4DS	4DL	5DS	5DL	6DS	6DL	7DS	7DL**
0	194	220	32	43	121	64	145	0	159	84	113	145	49

*Only the monotelosomic thus far available for test.
**In the variety Canthatch.

Morphology

The effects of most of the telocentrics on plant and spike morphology were indicated in a previous publication (E. Sears, 1954). Also McIntosh (1973) summarized the available data concerning the location of genes on particular arms, showing that at least one gene had been located to each of 29 of the 42 arms. Although a full description of the effects of each arm on morphology would presumably be useful, only a few comments are in order here.

In group 2, each chromosome carries a gene for awn promotion; this is on the short arm of 2A but on the long arm of 2B and 2D. (The 2DS, i.e., 2Dα-arm, was incorrectly identified as the carrier of the awn gene by E. Sears, 1954). The short arms of 2B and 2D both have a gene for waxy foliage, as McIntosh (1973) points out.

As expected from the characteristics of ditelo-1AL, spikes of ditelo-1AS are not greatly different from those of the nullisomic, except that they are marginally fertile. The fertility gradually decreases from bottom to top of the spike, with approximately the top half being sterile.

Ditelo-3AS (β) has spikes with somewhat longer awns than normal. Seeds are small.

Ditelo-6AL (β) is much nearer normal than -6AS. Both plant and spikes resemble normal rather closely. The same is true for ditelo-6DL (β). Ditelo-6BL, as previously noted (E. Sears, 1954), also is nearly normal in spike morphology, but unlike 6AL and 6DL, it is less fertile than the ditelosomic for the short arm.

As expected from the fact that ditelo-7AL, unlike nulli-7A, is non-pistilloid, ditelo-7AS has a tendency, not always expressed, toward pistillody.

Telosomic Stocks

Monotelosomics

Many of the telocentrics were first recovered as monotelosomics and have been maintained as such. Others were made monosomic by pollinating the monotelodisomic ($20'' + tl''$) by the ditelosomic for the other arm and then selfing the resulting double monotelosomic ($20'' + 2t'$). Among the offspring were numerous monotelosomics for each arm. A total of 25 monotelosomics are maintained (Table 7).

Ditelosomics and dimonotelosomics

As many as possible of the telocentric chromosomes, 34 in all, are maintained as ditelosomics (Table 7). They were obtained by selfing monotelosomics or monotelodisomics.

The remaining eight ditelosomics, with the possible exception of ditelo-1DS, are sterile. To each of these has therefore been added one dose of the telocentric for the other arm of the same chromosome. This restores fertility but of course results in segregation in each generation for the added monotelosome. All possible dimonotelosomics have been produced, except for the two involving 7DS and 7DL.

Double mono- and di-telosomics

A cross between the two ditelosomics for the same chromosome gives rise to double monotelosomics ($20'' + 2t'$), and these when selfed produce offspring that include a low frequency (usually less than 1/16) of double ditelosomics, In practice the double ditelos have usually been synthesized in two stages: Among the immediate offspring of double monotelo, a dimonotelo individual was selected; and this in the succeeding generation yielded relatively numerous double ditelos, often about 1/4 and seldom less than 1/16.

Table 7. Telosomic stocks available

	Monote-losomic	Ditelo-somic	Dimono-telosomic		Doub. di-telosomic	Doub. mono-telosomic
$1A^{S}_{L}$	x x	x x	x x	1A	x	x
$2A^{S}_{L}$		x	x x	2A	x	x
$3A^{S}_{L}$	x	x x	x x	3A	x	x
$4A^{\alpha}_{\beta}$	x	x	x x	4A	x	x
$5A^{S}_{L}$	x	x	x x	5A	x	x
$6A^{S}_{L}$	x x	x x	x x	6A	x	x
$7A^{S}_{L}$	x	x x	x x	7A	x	x
$1B^{S}_{L}$	x	x x	x x	1B	x	x
$2B^{S}_{L}$	x*	x	x x	2B	x	x
$3B^{S}_{L}$	x	x x	x x	3B	x	x
$4B^{S}_{L}$	x	x	x x	4B	x	x
$5B^{S}_{L}$	x	x	x x	5B	x	x
$6B^{S}_{L}$		x x	x x	6B	x	x
$7B^{S}_{L}$	x x	x x	x x	7B	x	x
$1D^{S}_{L}$	x	x	x x	1D	x	x
$2D^{S}_{L}$	x	x x	x x	2D	x	x
$3D^{S}_{L}$	x x	x x	x x	3D	x	x
$4D^{S}_{L}$	x* x	x x	x x	4D	x	x
$5D^{S}_{L}$	x	x	x x	5D	x	x
$6D^{S}_{L}$	x	x x	x x	6D	x	x
$7D^{S}_{L}$	x x**	x x**		7D		

*Seed supply very small. **In the variety Canthatch.

Two of the six telocentrics (2BS and 5DS) that had arisen in varieties other than Chinese Spring were combined with the corresponding complete chromosome of Chinese Spring and backcrossed for one or more generations to euploid Chinese Spring. At the conclusion of backcrossing, the telocentric was combined with the telo for the other arm to produce the double mono- and then the double ditelosomic. Each of the other four telocentrics (6AL, 4BS, 2DL, and 7DL) of extraneous origin was first combined with the second telocentric of the chromosome concerned, if not already so combined, and then crossed and backcrossed to Chinese Spring. Following the final backcross, a selfing of a double-telo trisomic ($20'' + tlt''$) gave rise to about one-fourth double ditelosomics, and one of these crossed as male to the appropriate monosomic yielded the double monotelosomic.

Uses

Identification of aneuploids and other aberrant types

The identification of monosomics was the first use to which wheat telocentrics were put. Determining whether or not two monosomic plants involve the same chromosome requires crossing the two and recovering a nullisomic or a double monosomic, a test which may require as many as 50–100 F_1 individuals. But when one of the monosomes is telocentric (or is an isochromosome) and is used as male in a cross to the other monosomic, the occurrence of monotelosomic offspring establishes that the same chromosome is involved in the two lines; and the frequency of such offspring is about 75%.

Now that ditelosomics are available, these are used in preference to monotelosomics, because they are more nearly stable and they do not have to be used as male to insure transmission of the telosome. Still better are the double ditelosomics, which are not only reasonably stable but are also of normal fertility.

Trisomes and tetrasomes are easily identified by the occurrence of a monotelotrivalent in the cross to the critical ditelosomic.

Which chromosomes are involved in reciprocal translocations is determined by crossing with ditelo- or double ditelosomics. If ditelos are used, the critical crosses show a chain of four, including a terminal telocentric, instead of a ring of four. With double ditelos, the two critical crosses have a chain of five, with a telocentric at each end.

In transferring characters to wheat from related species, a segment of one of the chromosomes of the alien species is sometimes substituted for a segment of a wheat chromosome. If the alien segment is large enough that the arm concerned pairs rarely or not at all with the corresponding wheat arm, the chromosome concerned can easily be identified by crossing with the double ditelosomics: In the critical cross only one of the two telocentrics pairs regularly, whereas in the non-critical crosses the telocentrics regularly constitute two members of a trivalent, almost always V-shaped at MI. If the non-pairing telo in the critical cross is not identifiable, separate crosses with the two ditelos of the chromosome concerned will reveal which arm is replaced in the transfer line.

Avoiding univalent shift

Whenever an ordinary monosomic plant is used in a cross or is allowed to self, a small fraction of its offspring are monosomic for a chromosome other than the parental monosome. This is because there is an appreciable frequency of pairing failure in common wheat, which leads to chromosome loss. Thus a gamete may carry the chromosome that was monosomic but by chance lack one of the other 20 chromosomes. Although the frequency of univalent shift should not exceed 1% unless the frequency of sporocytes with one or more non-synapsed bivalents is 6% or more, higher rates of asynapsis are not uncommon in intervarietal hybrids, particularly if grown at unfavourable temperatures; and any risk of shift, however low, should not be borne if it can be easily avoided. When the monosome is telocentric, shift results in a cytologically easy-to-recognize plant with a complete monosome and a heteromorphic bivalent (20″ + tl″ + 1′). For avoiding shift, monoisosomics and double monotelosomics are equally as useful as monotelosomics.

Somewhat related to univalent shift is the fact that in crosses of two homologous monosomics, in a few monosomic offspring the chromosome concerned comes through the egg rather than the pollen. This is because up to 10% of the functioning male gametes lack the chromosome that was monosomic, and about 25% of the eggs carry it. If the resulting small fraction of maternally derived monosomes among the progeny can be identified, intervarietal substitutions of chromosomes are relatively easy to make. Such identification is simple when the maternal monosome is telocentric.

Locating genes

The characteristics of a particular mono- or ditelosomic reveal directly what genes are located on the missing chromosome arm of the variety concerned. Most genes in other varieties are easily assigned to the correct arm by crossing with the two telosomic lines for the chromosome concerned and analyzing the F_1 gametes (in backcross or F_2) for transfer of the gene from the complete chromosome to one of the telocentrics. Of course it can only be transferred to the telocentric that carries the locus concerned. The combined frequency of telocentrics transmitted that carry the gene and of complete chromosomes that lack it is a direct measure of the frequency of crossing-over between the gene and the centromere. Thus telocentrics serve as very valuable tools for constructing linkage maps.

Determination of cytological characteristics

One of the standard identifying characteristics of a chromosome is the relative lengths of its two arms. These values were roughly determined (E. Sears, 1954; Morrison, 1953) for the variety Chinese Spring by measurement of a few monosomes of each chromosome at TII. The reliability of these measurements was not high, not only because of the small numbers of each chromosome measured, but also, particularly for chromosomes with nearly equal arms, because there was usually no way of distinguishing between the two arms except by their length. Where the arms were of nearly

equal length, one arm presumably measured longer in some cells, while the other arm was the longer in other cells, but the average of all the longer values was taken as the length of one arm and the average of all the shorter values as the length of the other.

Material now available—namely, the dimonotelosomics—permits a more accurate determination of the relative lengths of the arms. In root-tip cells of dimonotelo plants, there are two doses of one telocentric and one of the other. By measuring all three telos in each of a substantial number of cells, L. Sears (Wheat Newsl. **22**:95. 1976) found that two averaged nearly the same length, while the third was significantly longer or shorter. In roots of the complementary dimonotelo, with two doses of the opposite arm, the two telos of similar length were now shorter instead of longer, or longer instead of shorter. The averages were then used to calculate the relative lengths of the two arms. This method also tends to exaggerate slightly the differences in length between nearly equal arms but does not allow two equal arms to be classed as unequal. Only one chromosome, 4A, has arms so nearly equal in length that no significant difference could be found between them.

The development of procedures for differential staining of chromosomes allowed Gill and Kimber (1974) to characterize each chromosome of hexaploid wheat as to its bandedness following Giemsa staining. In order to be able to recognize each chromosome, these workers used ditelosomics, which could be identified even in broken cells with less than the complete complement of chromosomes.

Chromosome pairing and somatic association

The regularity with which any two homologues pair and the pattern of chiasma formation in each of the arms of the bivalent concerned are best determined with the aid of telocentric chromosomes. The frequency of pairing and the numbers of chiasmata formed are easily observed in ditelosomics, and Sallee and Kimber (1978) and Kimber and Hulse (1978) have shown that the pairing characteristics of each normal bivalent can be predicted with reasonable accuracy from the pairing of the two ditelosomes concerned. This is true in spite of the fact that crossing-over is reduced near the centromere of telocentrics (Endrizzi and Kohel, 1966; E. Sears, 1972b). Sallee and Kimber (1978) suggest that chiasmata near the centromere are not cancelled in telocentric pairs but are simply shifted distally.

Feldman *et al.* (1966) and Feldman and Avivi (1973) have shown that homologous chromosomes tend to lie closer together in somatic cells than do non-homologues. Such studies require cytologically identifiable chromosomes, and in wheat this has meant the use of telocentrics.

Transfer of alien genes

In transferring genes to wheat from other species and genera, it is presumably desirable that the introduced segment carrying the gene concerned be as short as possible.

This reduces the probability that it will include unwanted genes as well as the desired one. Through induced homoeologous pairing, however, a short segment cannot be obtained in one step, unless the gene concerned happens to be located near one end of the alien chromosome, because transfer of a short segment requires two crossovers close together—a rare event even in homologous exchange. What is needed is two exchanges on opposite sides of and close to the gene. When these two recombinants are combined, a crossover between them will give rise to a chromosome with the desired short alien segment carrying the gene concerned.

If a telocentric derivative of the alien chromosome is available for the induced crossing-over with the wheat homoeologue, this greatly simplifies distinguishing between the recombinants on opposite sides of the gene (E. Sears, 1977). Alternatively, if the wheat arm homoeologous to the critical alien arm is known, it, instead of the alien arm, can be the telocentric.

Correlation of chiasmata with crossing over

By combining the proper telocentric with a complete chromosome having the terminal portion of one arm replaced by an alien segment carrying a marker gene, Fu and Sears (1973) were able to show a correspondence between the frequency of pairing (i.e., chiasma formation) and the amount of crossing over.

Determining the relatedness of chromosomes and chromosome arms

The ability of chromosomes to pair with each other is considered a good measure of their degree of relatedness. The chromosomes of the wheats and their relatives vary all the way from apparent full homology to weak homoeology, with very little pairing even in the absence of the inhibitor of homoeologous pairing, *Ph.* In all cases of less than full homology, telocentric chromosomes are used to compare the degrees of relationship of the wheat chromosomes concerned to each other or to the alien chromosomes. Thus Feldman (1966) and Winkle (1976) showed that there was great variation in the pairing affinity of different A- and B-genome arms with *T. timopheevii* chromosomes, but that on the average those of the B genome paired less often.

It has generally been assumed that the long arms of homoeologous wheat chromosomes are homoeologous with long arms, and short arms with short arms. However, the presence of duplicate or homoeoallelic genes on arms that do not correspond in relative length, as 4B and 4D, has rightly been considered more critical evidence of homoeology. Of presumably even greater importance are data on the ability of two arms to pair, because there are surely several and probably many gene homologies involved in the pairing of any two arms.

In order to obtain pairing of homoeologous arms in useful frequency, it is necessary to suppress the action of *Ph.* This is easily done, as Riley and Chapman (1964, 1966) showed, by crossing with certain lines of *Triticum* (*Aegilops*) *speltoides.* Two ditelosomics from homoeologous chromosomes are first crossed together to produce

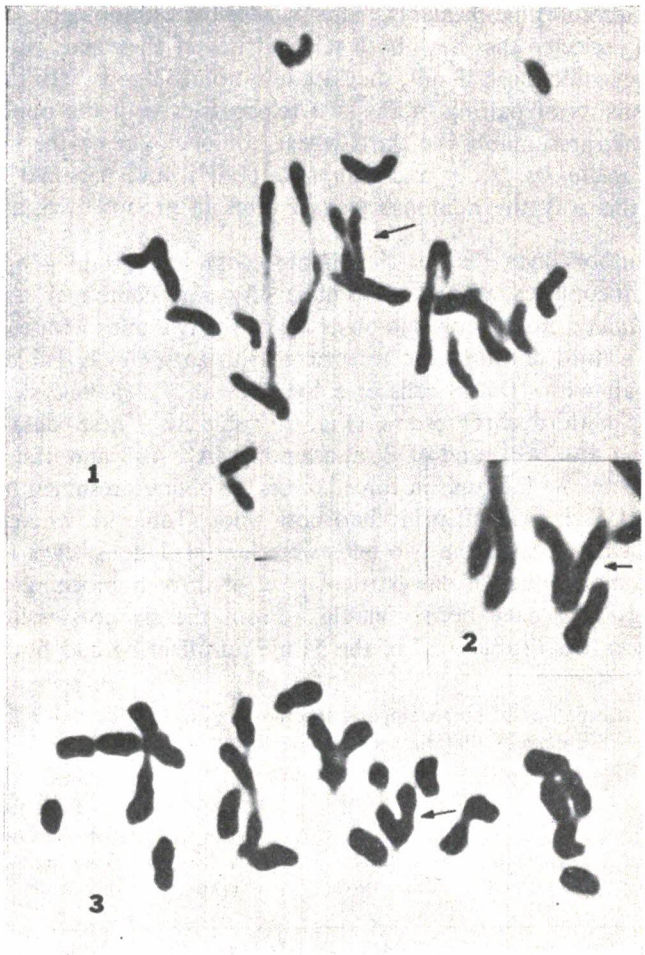
a plant with two heteromorphic bivalents. This plant is then pollinated by *T. speltoides* and hybrid offspring selected that have both telocentrics. If these pair with each other, they are judged homoeologous; if not, they are non-homeologous. In the latter case, further evidence consists of pairing of the two telocentrics with the opposite arms of another chromosome, presumably the third wheat homoeologue or the homoeologous chromosome of *T. speltoides*. Riley and Chapman (1964) and personal communication) identified in this way the homoeologies of arms in groups 5, 6, and 7.

The junior author finds that pairing homoeologies in group 4 agree with the evidence from homoeoalleles. When telocentric 4Aα was combined with 4BS in a hybrid with *T. speltoides,* no pairing was observed of the two telos with each other, but they did pair with a third chromosome to form a trivalent (Fig. 1, Table 8). Further, telo-4Aα did not pair with 4DL in cells of a hybrid with *T. speltoides,* but did pair simultaneously with a third chromosome (Fig. 2, Table 8). These data confirm the homoeologies among 4Aα, 4BL and 4DS, and among 4Aβ, 4BS and 4DL. Additional evidence is provided by the fact that in three crosses involving presumed homoeologous telocentrics, none of 33 hybrid offspring had both telos (Table 9), whereas 25% were expected to have them. Because the two telos were homoeologous, eggs receiving both of them had only one member of one particular set of three homoeologous arms, and therefore these eggs may have been inviable. From the six crosses involving non-homoeologous telocentrics (Table 9), 7 of the 54 hybrid offspring had both telos.

Table 8. Pairing of telocentrics of homoeologous chromosomes in hybrids with a line of *Triticum speltoides* that induces homoeologous pairing

Chromosomes	No. cells examined	Neither telo paired	One telo paired	Both telos paired	
				Two het. bivalents	Ditelo trivalent
2AL, 2BL	200	133	53	14	0
2AS, 2DL	196	126	63	3	4
4Aα, 4BS	613	489	121	2	1
4Aα, 4DL	31	21	0	0	2

Significant data for group 2 were obtained only for 2AS and 2DL (Table 8). These two telos participated in ditelo trivalents (Fig. 3) and therefore may be considered non-homoeologous. A hybrid involving 2AL and 2BL showed no pairing of the two telocentrics with each other or with the same other chromosome, although both were paired in 14 cells. Thus the possibility remains that the long arm of 2B is homoeologous with the short, rather than long, arms of 2A and 2D. The data concerning simultaneous transmission of two telocentrics (Table 9) are insufficient to demonstrate the homoeologies of 2BS and 2BL, but the occurrence of one hybrid plant carrying both 2AL and 2BL is supportive of these being non-homoeologous arms.



Figs. 1–3. First meiotic metaphase in hybrids of *Triticum aestivum* with *T. speltoides* in which two wheat homoeologues are represented only by telocentric chromosomes. In each case a ditelo trivalent (arrows) indicates that the two telocentrics are non-homoeologous. Fig. 1: telos 4A$^{\alpha}$ and 4BS. Fig. 2: 4A$_{\alpha}$ and 4DL. Fig. 3: 2AS and 2DL.

The relationships of the arms of an alien chromosome with those of one of its wheat homoeologues can be determined in essentially the same way as for two wheat chromosomes (Johnson and Kimber, 1967; Kimber, 1968; Athwal and Kimber, 1972). Either an addition telosomic or a substitution telosomic may be used. A cross with a wheat ditelosomic combines the alien and one wheat telo in a single plant, which is then pollinated by *T. speltoides*. As with two wheat telos, pairing of the two with each other shows homoeology, whereas their pairing with opposite arms of another chromosome shows non-homoeology.

Table 9. Chromosome constitution of offspring of plants with 19″ + tl″ + tl″ pollinated by *Triticum speltoides*

Telocentrics involved	Relationship	No. of offspring	No. with both telos
2AS, 2DL	Non-homoeologous	11	2
2AL, 2DS	,, ,,	2	0
2AL, 2BL	?	2	1
2BS, 2DS	?	5	0
2BL, 2DL	?	5	0
4Aα, 4BS	Non-homoeologous	31	5
4Aβ, 4BL	,, ,,	5	0
4Aα, 4DL	,, ,,	11	2
4Aβ, 4DS	,, ,,	1	0
4BL, 4DL	,, ,,	5	0
4BS, 4DS		1	0
4Aα, 4BL	Homoeologous	12	0
4Aα, 4DS	,,	5	0
4BL, 4DS	,,	16	0

Secondary association of monotelosomic bivalents at meiosis has been used as an indicator of relationship between the chromosomes concerned (Riley, 1960). Having each of two bivalents identifiable permits the scoring of MI plates for the number of other bivalents intervening between the two marked ones.

The association of telosomes in somatic cells is a possible method for identifying homoeologous chromosomes. However, a substantial degree of association can be expected only if *Ph* has been deleted or suppressed (Feldman and Avivi, 1973). This is most easily accomplished by crossing with *T. speltoides,* and the resulting double-monotelo hybrid plants will ordinarily be more easily assayed for pairing of the telos at meiosis than for association of the telos in somatic cells.

Discussion

Since the measurements of the two telocentrics of chromosome 4A in root-tip cells revealed no significant difference in length, it was assumed that in the previously reported TII measurements (E. Sears, 1954), the 13% difference in arm length noted was an artifact—that there was actually no difference, but that in each of the three TII cells measured one or the other arm happened to be longer and was recorded as the longer arm. However, it is also possible that the arm ratio of this chromosome is different in root-tip and TII cells, as Larsen and Kimber (1973) found for chromosome 5B. One other chromosome, 6A, has arms of so nearly the same length that its α arm might measure longer instead of shorter than β at TII.

Whereas monosomics are difficult to maintain in tetraploid wheat, telocentrics for certain arms may be easily maintained along with the corresponding complete

chromosome (Okamoto, 1961, Nishikawa, 1970), and double ditelosomics must be viable, fertile, and highly transmissible (Tsunewaki, 1963). Telocentrics can be used for some of the same purposes as in the hexaploid.

It seems highly desirable that the designations of the chromosome arms reflect their relatedness. This objective is not achieved by the present L and S designations as they apply to group 4 and possibly group 2. In group 4, the two arms of chromosome 4A are apparently not distinguishable on the basis of their length and therefore are called α and β. Further, the homoeologies of the other two chromosomes do not correspond with arm length. In group 2, chromosome 2B may be anomalous in the homoeologies of its arms with 2A and 2D.

We believe that the most reasonable solution to this problem is to give the arms new designations on the basis of their homoeologies. We suggest the use of the letters p and q, with p being used for the short arms in groups 1, 3, 5, 6, and 7, where there is agreement between length and homoeology. In group 2, 2AS and 2DS would become 2Ap and 2Dp, and whichever arm of 2B is homoeologous to 2AS and 2DS would be designated 2Bp. In group 4, 4Aα, 4BL, and 4DS should presumably be the p arms. Since the arms of 4A are of equal length, the allocation of p and q must be based on 4B or 4D, and 4D is preferred because it is more closely related to 4A than is 4B, on the basis of the similarity of nullisomics 4A and 4D and the somewhat greater ability of tetrasome 4D to compensate for nullisome 4A.

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Note added in proof: There is evidence that what we have called telo-1DS is actually a proximal fragment of 1DL, and we are, therefore, looking for a true telo-1DS.