THE IDENTIFICATION OF ANEUPLOID LINES AND A STUDY OF SOMATIC ASSOCIATION IN *AVENA SATIVA* L.

A THESIS

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ABSTRACT

Several aneuploid lines of common oats, Avena sativa L., were studied to identify the chromosomal deficiencies in relation to the standard karyotype. Two ditelosomic, four monosomic and two nullisomic lines were identified.

A line ditelosomic for chromosome 20^{L} and two isolates ditelosomic for chromosome 21^{L} were identified by cytological and karyotype analyses respectively. Three previously identified lines monosomic for chromosome 7, 10 and 20 were found to be deficient for the same chromosome, namely 20. The gene for normal vs. abaxial curling of the leaves was associated with the short arm while the diploidisation gene was associated with the long arm of chromosome 20. The gene for normal vs. kinky neck was also confirmed to be on 20^{L}.

One line monosomic for chromosome 6, one for chromosome 10, two for chromosome 21 and two lines nullisomic for chromosome 15 were identified by cytological and karyotype analyses.

The reciprocal translocation present between the variety Sun II and Garry and Rodney does not involve the following chromsomes 4, 6, 12, 14, 15, 18 and 20.

A study of somatic association of the chromosomes in Avena sativa was conducted. Root tip cells were examined at mitotic metaphase, and distances between homologous as well as between non-homologous chromosomes were measured and their frequency distributions compared. Non-homologous chromosomes were scattered at random in the cells studied. In contrast, the mean distance between homologous chromosomes was significantly shorter indicating a tendency for somatic association of homologues in this species.

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INTRODUCTION

Avena sativa L. is an allohexaploid species with $2n = 6x = 42$ chromosomes comprising three genomes, namely A, C and D. Due to the polyploid nature of common oats, the deficiency of a whole chromosome or a pair of homologous chromosomes can be tolerated, and it should be possible to produce a monosomic and nullisomic series of 21 different lines. In wheat, also an allohexaploid, a monosomic series was developed by Sears (1939) from the progeny of a haploid plant and a partially asynaptic line. He also established the related nullisomic and ditelosomic series (Sears, 1954).

In wheat, ditelosomic lines have been used to verify monosomic identification, for linkage mapping (Sears, 1963) and in somatic association studies (Feldman *et al.*, 1966). A telocentric chromosome includes a functional centromere plus one complete arm of a normal chromosome. Telocentrics usually arise by misdivision of unpaired chromosomes at meiosis (Morris and Sears, 1967).

A monotelosomic plant has one arm of a chromosome replacing a pair of homologous chromosomes; its meiotic configuration is 20 bivalents plus one telocentric univalent. Ditelosomics arise in progeny of self-pollinated monotelosomic plants. Because of their meiotic stability and fertility, ditelosomics are useful tools to carry out cytogenetic studies.

Thus far, a total of 19 different monosomic lines have been identified in *Avena* by different authors. Spontaneous and induced aneuploids have been the main sources of monosomics studied. Interline crosses have been used to determine the homology of monosomic lines whose

univalent chromosomes appeared similar from critical karyotype analysis. No attempts have been made to obtain ditelosomic lines from the monosomic lines already identified though monotelosomics were obtained and used to associate phenotypic changes with specific arms of chromosomes.

Association of homologous chromosomes in somatic cells has been reported in a number of organisms. Somatic association of homologues can be studied in common oats because a number of chromosomes are readily identifiable. Chromosome pair 21 (shortest of the complement) and a pair of telocentrics other than 21 are ideal material for such a study. By comparing the frequency distributions of the distances between homologous and non-homologous chromosomes, any attraction between homologues can be established.

The present study is concerned with three major phases: (1) the identification of aneuploid lines available at this institution with the view to completing the monosomic series; (2) the identification of ditelosomic lines and the association of known markers with specific arms of chromosomes; and (3) an investigation of somatic association of homologous chromosomes in the species.

LITERATURE REVIEW

The establishment of a monosomic series in hexaploid oats was facilitated by the use of a standard karyotype proposed by Rajhathy (1963). Previous studies consisted of association of phenotypic changes with chromosomal deficiencies, each worker using his own system of nomenclature for the chromosomes involved. No relationship existed between the various systems of nomenclature and the results could not be compared. This review, therefore, will only cover the studies made in relation to the standard karyotype and those which can be related to it through recent findings.

Present status of aneuploid investigations.

A total of 19 monosomic lines have been identified according to the standard karyotype. The chromosomes still awaiting identification are 11 and 16. Table 1 shows the aneuploid characteristics specifically resulting from the loss of one chromosome or a pair of homologous chromosomes. The arm of the chromosome responsible for the characteristic has been identified in some cases. The aneuploid characteristics are described as seen on nullisomic plants except for neck kinkyness, side-panicles and white striations on the leaves where the monosomic plants also demonstrate the phenotype due to the dominance of the deletion in the hemizygous condition.

Other phenotypic effects such as low fertility, shorter straw, lack of vigor, smaller panicles, retarded growth, etc., are produced by the loss of a number of chromosomes or chromosome pairs.

Duplication of genetic functions are common in polyploid species. Several chromosomes in hexaploid oats produced similar phenotypic and

Table 1. Identified monosomics and gene-chromosome association.

*Induced aneuploids.

Chromosome	Arm	Origin	Aneuploid characteristics	Authority
1	-	Sun II	Glaucous Complete asynapsis (control early phases of meiotic pairing)	Hacker & Riley, 1965
2	-	Sun II	Asynapsis Abaxial curling of leaves and Kinky neck	Hacker & Riley, 1965
3	short	Victorgrain* (*A. byzantina*)	Sterility (normal meiotic behavior) Dosage effects for dark grey color of lemmas	Singh & Wallace, 1967
4	-	Garry*	Narrow leaves	Sun, 1965, Lin, 1968
	-	Russel x *A. strigosa*	Albino Homoeologous to 15 and 21	McGinnis *et al.*, 1968
5	-	-	---	Rajhathy (personal communication)
6	-	Garry*	None	Sun, 1965.
7		Rodney*	Abaxial curling of the leaves	Gauthier, 1967
	long - -	Rodney*	Kinky neck Complete sterility Reduced chiasma frequency in one genome	Gauthier, 1967
	-	Rodney*	Diploidisation gene Frustated panicles	Gauthier, 1967
	-	Victorgrain*	Complete asynapsis Control the pairing of one genome	Singh and Wallace, 1967

continued.....

Chromosome	Arm	Origin	Aneuploid characteristics	Authority
8	-	Garry*	Large necrotic spots on leaves	Gauthier, 1967
9	-	Garry x Rodney	None	Lin, 1968
10	-	Garry*	None	Gauthier, 1967
11	-	-	No reported aneuploids	-
12	short	Garry*	Non-synchrony in anther and stigma maturity	Gauthier, 1967
13	short	Garry*	Inhibitors of fatuoid phenotype	Gauthier, 1967
	-	Garry	Neck kinkyness	Gauthier, 1967
	short	Victorgrain*	Desynapsis in two genomes	Singh & Wallace, 1967
	short	-	Asynapsis	Huskins & Hearne, 1933
	short	Victory	Fatuoid phenotype	Nishiyama, 1933
	long	Garry*	Asynapsis	Gauthier, 1967
	long	Victorgrain*	Fatuoid phenotype	Singh & Wallace, 1967
	long	Victory	Desynapsis	Nishiyama, 1933
	-	Sun II	Fatuoid phenotype Desynapsis	Hacker & Riley, 1965

continued.....

Chromosome	Arm	Origin	Aneuploid characteristics	Authority
14	long	Garry*	Abaxial curling of leaves White striations on leaves Fatuoid expression when part of chromosome 19^S is deleted	Sun, 1965
	long	Sun II	A two gene control of chlorophyll synthesis	Hacker, 1966
	-	Rodney*	Abaxial curling of leaves Secondary florets enclosed in primary lemmas Pubescence on primary lemmas Semi-abscission of the spikelet	Gauthier, 1967
		Garry x Victoria	Partial asynapsis Nuda Multiflorous spikelets Elongated rachilla of the first floret	Lin, 1968
15	-	Garry*	None	Sun, 1965
	-	Sun II	Thick culms	Hacker & Riley, 1965
	-	Sun II x Rodney	None	Lin, 1968
	long	White Russian x Exeter (F_3)	Albinism	McGinnis & Andrews, 1962
	-	Garry	Side panicles Thick stems	McGinnis & Lin, 1966

continued.....

Chromosome	Arm	Origin	Aneuploid characteristics	Authority
16	-	-	No reported aneuploids	--
17	-	Victorgrain*	Protandry Awns on primary and secondary florets Green floret base	Singh & Wallace, 1967
18	long	Garry*	Kinky neck Reduce spikelet size Compact and upright spikelets	Sun, 1965
19	short	-	Weak inhibitor of fatuoid expression when chromosome 14 is in nullisomic condition	Sun, 1965
	-	-	---	Rajhathy (personal communication)
20	long	Garry	Kinky neck	Gauthier, 1967
	-	Sun II x Rodney	None	Lin, 1968
		Garry x Victoria	None	Lin, 1968
21	-	Rodney*	Albinism	Gauthier, 1967
	-	Garry*	None	Sun, 1965
	-	R.L. 1574 x Ripon	Albinism	McGinnis & Taylor, 1961
	long	Rodney^5 x Exeter	Albinism	McGinnis et al., 1963
	-	Sun II	None	Hacker & Riley, 1965
			Homoeologous to 4 and 15	McGinnis et al., 1968

meiotic changes such as albinism, abaxial curling of the leaves, neck kinkyness and control of pairing.

Albinism.

Nullisomy of chromosome 4, 15 and 21 produces albinism. McGinnis et al. (1968) suggested that these chromosomes comprise a homoeologous series carrying the V_3, V_2 and V_1 genes respectively responsible for chlorophyll production.

Abaxial curling of the leaves and neck kinkyness.

Abaxial curling of the leaves and neck kinkyness are two other phenotypic changes associated with the loss of several chromosome pairs. These phenotypic changes are also expressed mildly in monosomics. Abaxial curling of the leaves was associated with chromosome 2 (Hacker and Riley, 1965), 14 (Sun, 1965), 7 (Gauthier, 1967). Neck kinkyness was associated with chromosome 2 (Hacker and Riley, 1965), 18 (Sun, 1965), 7 and 13 (Gauthier, 1967) and 20 (Gauthier and McGinnis, 1965). Gauthier and McGinnis (1965) associated the genetic factor for normal neck-shape on the long arm of chromosome 20.

Synapsis.

Synapsis is influenced by several chromosomes. Nishiyama (1933) located a synaptic factor on the long arm of the "C" chromosome while Huskins and Hearne (1933) located it on the short arm. Gauthier (1967) working with a fatuoid line in the variety Garry tentatively identified the "C" chromosome as 13 and located an asynaptic factor on the long arm. Singh and Wallace (1967) also working with an aneuploid line expressing the fatuoid phenotype in the variety Victorgrain located a

desynaptic factor on the short arm of chromosome 12 or 13. They concluded that the nullisomy of chromosome 12 or 13 resulted in desynapsis of two genomes by controlling the later steps in the pairing processes and movements of the chromosomes belonging to the C and D genomes.

Hacker and Riley (1965) working with naturally occurring aneuploids in the variety Sun II identified two monosomic lines for chromosome 1 and 2. Nullisomy of chromosome 1 resulted in complete asynapsis with 40 univalents regularly seen at metaphase I and nullisomy of chromosome 2 resulted in partial asynapsis leading to a mean pairing of 4 bivalents and 32 univalents at metaphase I of meiosis.

Singh and Wallace (1967) reported that nullisomy of chromosome 7 caused asynapsis. Chromosome 7 controls the pairing of all chromosomes but more specifically the 14 chromosomes belonging to the A genome. Gauthier (1967) working with irradiated material from Avena sativa var. Rodney identified two isolates monosomic for chromosome 7. This chromosome also had an influence on the pairing of the chromosomes of the genome it belongs to by reducing the chiasma frequency in 6 bivalents. In a nulli-haploid plant, the absence of chromosome 7 resulted in a high number of multivalents which could be explained by the presence of a diploidisation gene on chromosome 7 (Gauthier and McGinnis, 1968).

Schulenburg (1965), in an aneuploid line for a chromosome in the group 16 - 20, found that nullisomy of the chromosome resulted in partial asynapsis (7^{II} and 26^{I}) at metaphase I of meiosis.

Somatic Association.

At mitotic interphase the nucleus appears as a mass of chromatin without any form of organisation. Yet, at the onset of cell division,

the chromatin arranges itself into chromosomes which separate to opposite poles of the cell with great precision. At meiosis, the homologues regularly pair together, form chiasmata and segregate to opposite poles. Such precision is more understandable if the homologues are actually lying close to each other in the interphase nucleus.

Association of homologous chromosomes in somatic cells has been reported in a number of organisms, namely Crepis capillaris (Kitani, 1963), Dipterans (Metz, 1916), Man (Schneiderman and Smith, 1962), maize (Maquire, 1967), and wheat (Feldman et al., 1966).

Feldman et al., (1966) demonstrated that the homologues in wheat tend to lie closer to each other than expected by chance alone by measuring the distances between members of pairs of homologous and between non-homologous chromosomes in root tip cells and comparing the frequency distributions. They also demonstrated that in wheat the centromere was mainly responsible for the attraction by measuring distances between telocentrics of opposite arms of the same chromosome. Feldman (1966) studying the effect of chromosome 5B on meiotic pairing in wheat, found that homologous chromosomes are associated before meiosis begins. This and the somatic association of homologues in root tip cells suggest that somatic association is present throughout the life of the organism. Feldman (1966) also demonstrated that genes, located on homoeologous chromosomes 5A, 5B and 5D, regulate somatic association.

MATERIALS AND METHODS

The aneuploid lines used in the study were obtained from several sources and are outlined in Table 2. Special attention was given to the screening of monotelosomic plants in the progreny of selfed monosomics previously identified. Ditelosomic lines were derived by selfing monotelosomic plants.

For mitotic investigation seeds from aneuploid lines were placed on a moist blotter, cold-treated at 0 - 2°C for 2 weeks and germinated at 27°C for 24 hours. The young root tips were excised, placed in ice-chilled water (0 - 2°C) for 24 hours to accumulate metaphase figures and then fixed in Farmer's fluid (3 ethyl alcohol:1 acetic acid) for at least two days. After fixation the root tips were hydrolysed in 1N HCl for 10 minutes and stained with reduced basic Fuchsin. The stained meristematic tip was squashed between a slide and cover slip in either 1% acetocarmine or 45% acetic acid and the chromosomes counted. In the later steps of the study, acetic acid (45%) was used to improve the spreading of chromosomes at mitotic metaphase, thus facilitating karyotype analysis. Karyotype analysis was made on the best fresh preparations, both by direct examination and by photomicrographs where the chromosomes could be cut out and organized according to the standard karyotype of Rajhathy (1963).

For meiotic studies young panicles, used to study pollen mother cells (PMC), were collected, fixed in Carnoy's fluid (6 ethyl alcohol: 3 chloroform:1 acetic acid) and squashed in 2% acetocarmine. The chromosome number determined from root tip counts was confirmed and in the case of mono and ditelosomic plants their pairing behavior was particularly noted.

Interline crosses were designed to check the homology of monosomic chromosomes. Lines monosomic for the same chromosome will give rise to

Table 2. List of aneuploid lines used in the study.

Line	Chromosome	Variety (X-ray dose)	Authority
Mono VIII	2	Sun II (spontaneous)	Hacker & Riley, 1965
M-3	3	Victorgrain (?)	Singh & Wallace, 1967
R-355	4	Garry (300r)	Sun, 1965
R-524	6	Garry (300r)	Sun, 1965
Rx - 742	7	Rodney (150r)	Gauthier, 1967
ST-7	7	Victorgrain (?)	Singh & Wallace, 1967
GR-27-106	9	Garry x Rodney	Lin, 1968
21-120	10	Garry (spontaneous)	McGinnis, unpublished
S-214	12	Garry (sonic vibrations, 20 min)	Gauthier, 1967
R-176	14	Garry (300r)	Sun, 1965
18-81	15	Garry (spontaneous)	McGinnis & Lin, 1966
Rx - 40	15	Rodney (75r)	McGinnis, unpublished
ST-17	17	Victorgrain (?)	Singh & Wallace, 1967
R-364	18	Garry (300r)	Sun, 1965
4-27	20	Garry (spontaneous)	Gauthier, 1967
Gx - 26	-	Garry (75r)	Andrews & McGinnis, 1964
Gx - 58	-	Garry (300r)	" " "
Gx - 69	-	Garry (300r)	" " "
Gx - 99	-	Garry (600r)	" " "
Gx - 154	-	Garry (600r)	" " "
Gx - 164	-	Garry (600r)	" " "
Gx - 240	-	Garry (600r)	" " "
Gx - 438	-	Garry (300r)	" " "
Gx - 623	-	Garry (150r)	" " "
R-127	-	Garry (300r)	" " "
R-365	-	Garry (300r)	" " "
Ditelo 3	-	Sun II (spontaneous)	Hacker & Riley, 1963
Ditelo 4/2	-	" "	" " "
Ditelo 21	-	" "	" " "
Ditelo 101	-	" "	" " "
Ditelo 102	-	" "	" " "
Ditelo 105	-	" "	" " "
Mono 8/1	-	" "	" " "
Mono 8/2	-	" "	" " "

20 bivalents in the 40-chromosome F_1 hybrids whereas if the monosomics are different the meiotic configuration will be 19 bivalents plus 2 univalents. In F_1, 40 + t-chromosome hybrids (monosomic x telosomic aneuploid), 20 bivalents plus a telocentric univalent indicate that the telocentric is one arm of the monosome under investigation; a heteromorphic bivalent and a full univalent plus 19 bivalents demonstrate that the telocentric is not homologous to the monosome used as female parent (Figure 1).

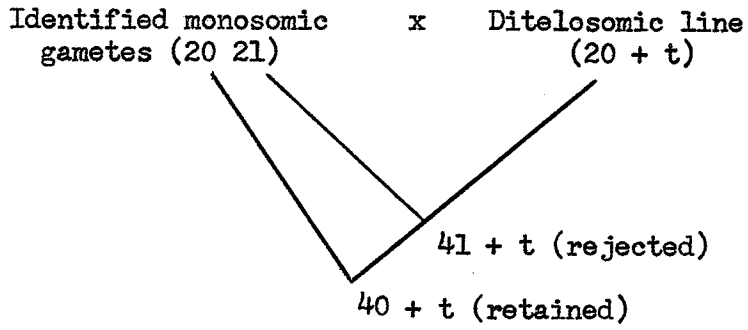
Hybrids between different aneuploids were produced by the introduction of yellowish anthers into florets emasculated one to five days prior to hand-pollination. Emasculated florets were bagged to prevent outcrossing. In interline crosses involving monosomics, the male parent was chosen on the basis of percent of nullisomic plants in its progeny. The higher the percent, the greater the chance of having 40-chromosome plants in the progeny of interline crosses. In crossing monosomic by telosomic aneuploids, telosomic plants were used as the male parent. The presence of a telocentric chromosome in the male gamete increases the frequency of the desired type of hybrids (40 + t-chromosome), thus reducing the effort of producing hybrid seeds.

The number of micronuclei per tetrad was scored to calculate the frequency of normal gametes produced. It was assumed that in tetrads where no micronuclei were present four 20 + t-chromosome pollen grains would be produced, where one micronucleus occurred the ratio would be 3 normal to 1 deficient gametes and where two micronuclei were found, two gametes would be deficient, etc.

To determine whether somatic association of homologues was present in common oats, a ditelosomic line (Ditelo 3) was used. The telocentrics

Figure 1.

Identification of ditelosomic lines



at meiosis, two (2) pairing patterns are possible:

1) $19^{II} + 1^{II}$ hetero + 1^{I}
(not the monosomic used)

2) $20^{II} + 1^{I}$ telo
(is the monosomic used)

were not identified but are not chromosome 21 since 21 bivalents always formed at meiosis, the telocentrics pairing together to form an open bivalent. The telocentrics could be differentiated from chromosome 21 by their terminal centromeres in somatic metaphase.

Distances between the midpoints of telocentrics, distances between centromeres of the chromosomes 21, and distances between the midpoints of the telocentrics and the centromeres of the chromosomes 21 were taken in the same cell (Plate 1). The distance between the two chromosomes farthest apart in the cell concerned was also taken to minimize the differences due to squashing.

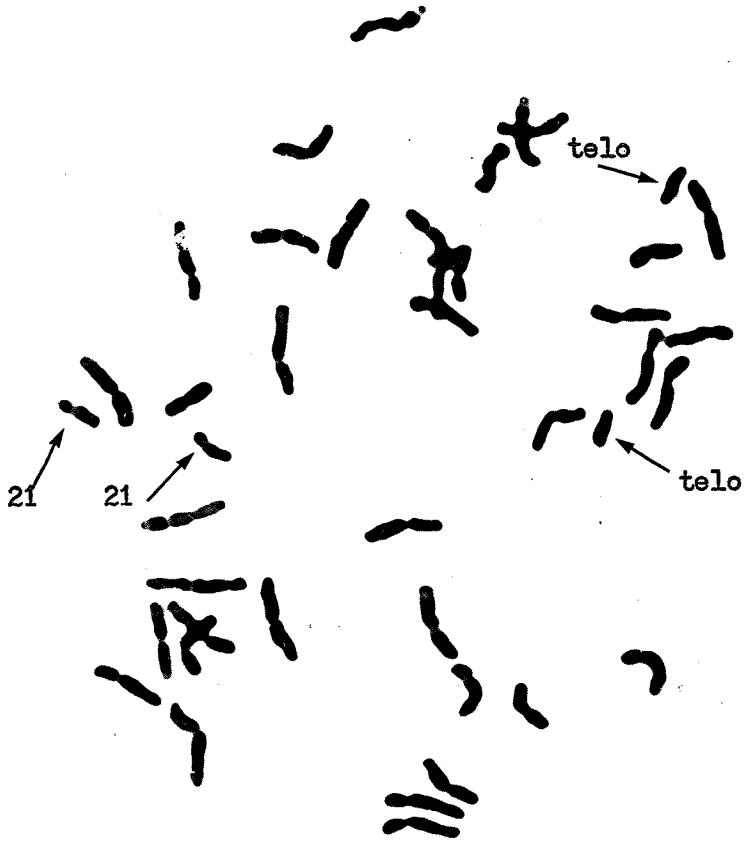
If we consider the non-homologous chromosomes as two points distributed at random in an area, the expected frequency distribution (Fig. 2A page 40) can be calculated by the substitution of a series of values from 0 to 1 in Hammersley's formula (taken from Feldman et al., 1966):

$$f(X)^{(\chi)} = \frac{16\,\chi}{\pi}\left[\cos^{-1}\chi - \chi(1-\chi^2)^{\frac{1}{2}}\right].$$

The mean and variance of such an expected distribution are 0.452 and 0.045, respectively. The Wilcoxon matched-pairs signed-ranks test was used for the statistical comparisons between the frequency distributions of distances of homologous and non-homologous chromosomes (Siegel, 1956). The Kolmorov-Smirnov one sample and two sample tests were used in the statistical comparisons of the frequency distribution of distances of non-homologous chromosomes with the theoretical frequency distribution of distances and in the comparison of the frequency distribution of distances of homologous chromosomes to each other (Siegel, 1956).

Plate 1. Typical somatic metaphase in a root tip cell where measurements were taken.

Magnification 600X.


telo
telo
21
21

RESULTS AND DISCUSSION

The results will be discussed in the order given in the introduction: (1) the identification of aneuploid lines; (2) the identification of ditelosomic lines; and (3) a study of somatic association of homologous chromosomes.

(1) Identification of aneuploid lines.

The results will be given in tables for brevity. The tables do not indicate the direction of the cross but the relevant information was given in materials and methods. The cross products are given at the intersection of the horizontal rows and vertical columns.

Table 3 lists the aneuploid lines used in the crosses and the number of F_1 interline hybrids studied meiotically in each individual cross. Table 4 with appendix gives the results of the metaphase I meiotic pairing studies on the F_1 interline hybrids. When possible, more than one F_1 interline hybrid was studied meiotically to reduce the possibility of artifacts caused by univalent shift.

Four monosomic lines R - 127, Gx - 164, Gx - 99 and Gx - 154 were found to be monosomic for chromosome 6, 10, 21, and 21, respectively. The lines R - 127 and Gx - 164 were crossed to R - 524 (monosomic-6, Sun 1965) and A - 411 (monosomic-10, Gauthier 1967), respectively. In both cases, the 40-chromosome F_1 hybrids showed a pairing of 20 bivalents (Table 4 appendix). The lines Gx - 99 and Gx - 154 proved to be deficient for chromosome 21 by karyotype analysis.

Among unidentified monosomic lines, Gx - 26, Gx - 58, Gx - 69, Gx - 438 and Gx - 623 proved to be deficient for a chromosome other than those listed in Table 5.

Table 3. The analysed crosses performed between aneuploid lines and the number of F_1 hybrids studied in each cross.

	R-355	GR-27-106	21-120	R-524	S-214	R-176	18-81	Rx - 742	ST-7	ST-17	R-364	4-27	Gx - 26	Gx - 58	Gx - 69	Gx - 438	Gx - 623	R-365	Gx - 240	Ditelo 3	Ditelo 4/2	Ditelo 21	Ditelo 101	Mono 8/1	Mono 8/2
	mono-4	mono-9	mono-10	mono-6	mono-12	mono-14	mono-15	mono-7	mono-7	mono-17	mono-18	mono-20	monosomic	monosomic	monosomic	monosomic	monosomic	monotelosomic	dideleted	ditelosomic	ditelosomic	ditelosomic	ditelosomic	ditelosomic	nullisomic	nullisomic
Gx - 26	3		1			2				1	2														
Gx - 58			1							2															
Gx - 69		1									2														
Gx - 438			2			3						1	2		1										
Gx - 623	1																								
R-365		1										2	2	4	2	2	2								
Gx - 240		1	1										3	1	2	2	2	1							
Ditelo 3	2	2	3	3	2	1	2	2		2	1	2	2		2	2	2								
Ditelo 4/2	2	2	2	3	2	1	2	3	2	2	2	4	2	1	2		2	2		2					
Ditelo 21			1	2	4	2	2	2	2	2	2	2	2	1	2	2	2	2	2	2	2				
Ditelo 101		1	2		2	1	2	2	2	1		2	2	1	1	2	3		2	2	2	2			
Mono 8/1		1	2		2	2	2	2			2	2		1			1					2	2		
Mono 8/2					2		2	2			1	2			3	1	1			1	2	2	1	2	

Table 4. Results of homology studies in hybrids between aneuploid lines.

A. The aneuploid lines are deficient for the same chromosome.

-. The aneuploid lines are deficient for two different chromosomes.

-*. The aneuploid lines are deficient for two different chromosomes by deduction.

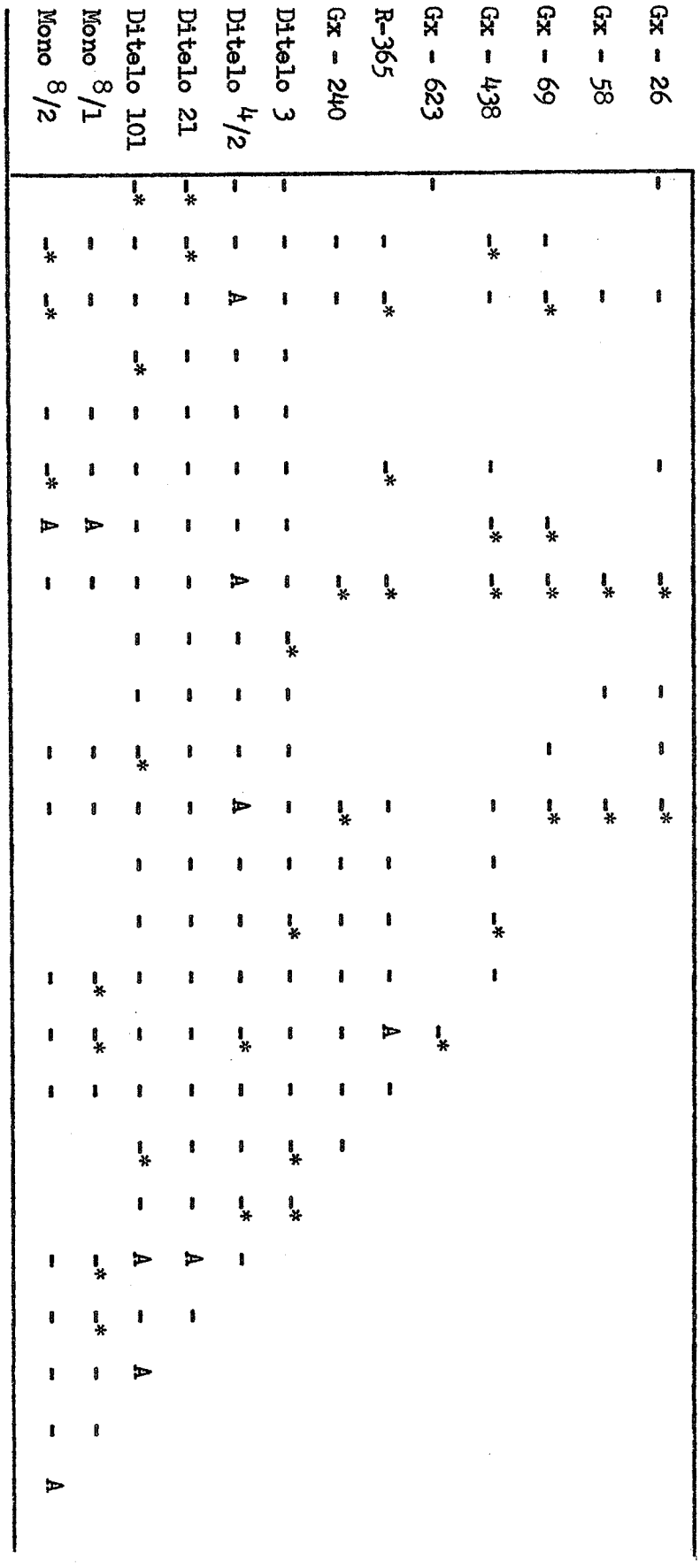

Gx - 26
Gx - 58
Gx - 69
Gx - 438
Gx - 623
R-365
Gx - 240
Ditelo 3
Ditelo 4/2
Ditelo 21
Ditelo 101
Mono 8/1
Mono 8/2
R-355 mono-4
GR-27-106 mono-9
21-120 mono-10
R-524 mono-6
S-214 mono-12
R-176 mono-14
18-81 mono-15
Rx - 742 mono-7
ST-7 mono-7
ST-17 mono-17
R-364 mono-18
4-27 mono-20
Gx - 26 monosomic
Gx - 58 monosomic
Gx - 69 monosomic
Gx - 438 monosomic
Gx - 623 monosomic
R-365 monotelosomic
Gx - 240 dideleted
Ditelo 3 ditelosomic
Ditelo 4/2 ditelosomic
Ditelo 21 ditelosomic
Ditelo 101 ditelosomic
Mono 8/1 nullisomic
Mono 8/2 nullisomic

Table 4 (appendix). Results of homology studies in hybrids between aneuploid lines.

Other crosses performed and analysed cytologically

Gx - 26 (41) x Rx - 40 (41 + t)
3 F_1 40 + t-chromosome, 19^{II} + 1^{II} hetero + 1^{I}

Gx - 58 (41) x M-3 (41)
1 F_1 40-chromosome, 19^{II} + 2^{I}

Gx - 69 (41) x Mono VIII (40) (chromosome 2)
1 F_1 40-chromosome, 17^{II} + 1^{IV} + 2^{I}

Gx - 69 (41) x M-3 (41)
1 F_1 40-chromosome, 17^{II} + 1^{IV} + 2^{I}

Gx - 623 (41) x 17-21 (41)
1 F_1 40-chromosome, 19^{II} + 2^{I}

Gx - 309 (41) x R-355
4 F_1 40-chromosome, few 20^{II} but mostly 19^{II} + 2^{I}

Rx - 40 (41) x 18-81 (41)
3 F_1 40-chromosome, 20^{II}

A-411 (41) x Gx - 164 (41)
(monosomic-10)
1 F_1 40-chromosome, 20^{II}

R-127 (41) x R-524 (41) (monosomic-6)
1 F_1 40-chromosome, 20^{II}

21-120 (41) x GR-27-106 (41) (monosomic-9)
(monosomic-20)
1 F_1 40-chromosome, 19^{II} + 2^{I}

Table 5. Non-identities of 5 monosomic lines.

Non-homology was concluded from:

K - karyotype analysis.

C - Cytological analysis.

P - Phenotype analysis.

C* - Cytological analysis by deduction.

(see Table 4)

	Chromosome												
LINE	1	2	3	4	8	9	13	14	15	ST-17	18	20	21
Gx - 26	K	K		C	K		P	C	C	C	C	C	K
Gx - 58	K	K	C		K		P			C		C	K
Gx - 69	K	C	C		K	C	P		C*		C	C	K
Gx - 438	K	K			K	C*	P	C	C*			C	K
Gx - 623	K	K		C	K		P		C*			C	K

A monotelosomic line (R-365) was deficient for the same chromosome as Gx - 438, an unidentified monosomic line, but the chromosome is not 1, 2, 8, 9, 13, 14, 15, 20 and 21 (Table 4).

Two nullisomic lines (Mono $^{8}/1$ and $^{8}/2$) were deficient for chromosome 15 when crossed with 18-81 (monosomic-15, McGinnis and Lin 1966) (Table 4). These lines did not show either albinism or side-panicle phenotypes known to be controlled by chromosome 15.

(2) Identification of ditelosomic lines.

(a) Ditelosomic for chromosome 20^{L}.

A ditelosomic line (Ditelo $^{4}/2$) was crossed to monosomic lines 4, 6, 7, 9, 10, 12, 14, 15, 18, 20 of A. sativa and ST-7 and ST-17 of Avena byzantina. The monosomics known as 1, 2, 8, 13 and 21 were excluded in the crosses because phenotypic and karyotype analyses revealed the presence of these chromosomes in the genomic complement of the ditelosomic line. The number of F_1 hybrids studied meiotically and the synaptic characteristics of the telocentric in each cross are shown in tables 3 and 4, respectively.

As illustrated in table 4 and plate 2, the crosses involving monosomic -7, -10 and -20 revealed a meiotic pairing where the telocentric was a univalent and all the other chromosomes were involved in associations. This indicates that the three previously identified monosomics -7, -10 and -20 are in fact monosomic for the same chromosome, namely 20. In the crosses involving the monosomics, other than 7, 10 and 20, the telocentric was always paired with a full chromosome forming a heteromorphic bivalent indicating non-homology between the telocentric and any of these other chromosomes.

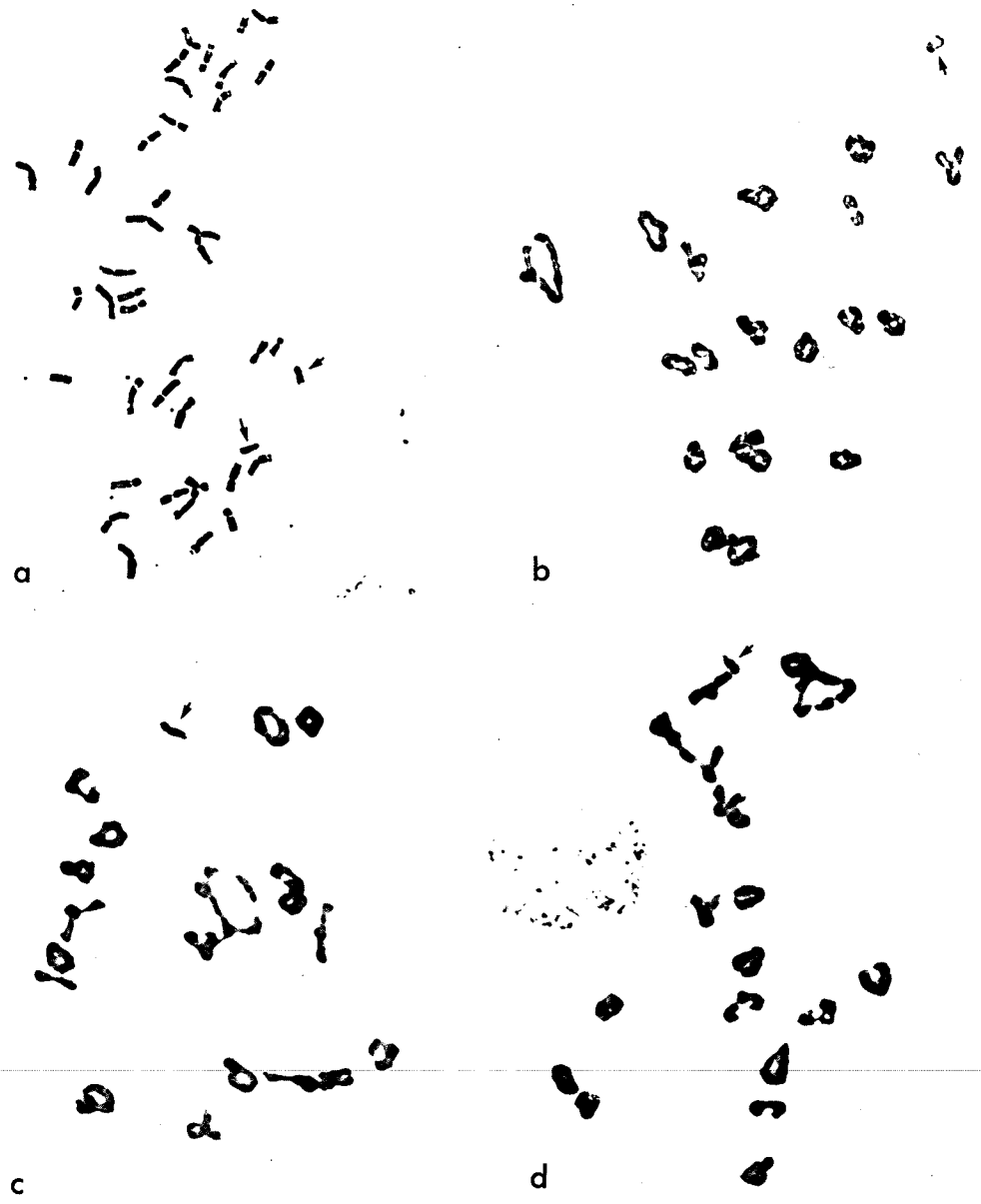
Lin (1968) suggested that Avena byzantina and A. sativa differed by at least two reciprocal translocations. In the present study, only the pairing behavior of the telocentric was recorded in the hybrids ST-7 and ST-17 by Ditelo $^{4}/2$ because univalents and multivalents were present at metaphase I.

Plate 2. Crosses involving monosomic-7, -10 and -20 and ditelosomic for 20^{L} showing the telocentric as a univalent.

a. Mitotic metaphase of ditelosomic-20^{L} (arrows).

b, c, d. Metaphase I of meiosis of the 40 + t hybrids between monosomic-7, -10 and -20 and ditelosomic-20^{L}, respectively.

Magnification 600X.


a
b
c
d

A heteromorphic bivalent was seen in all cells studied.

Hacker and Riley (1965) reported that nullisomics for chromosome 2 of Sun II had curled leaves and kinky necks. In the variety Garry, the genes for these two characters were located on chromosome 14 (Sun, 1965) and 20 (Gauthier and McGinnis, 1965), respectively. From this, Hacker and Riley (1965) suggested that chromosome differences between Sun II and Garry may be due to a translocation involving these chromosomes. Lin (1968) concluded that a reciprocal translocation involving two pairs of chromosomes was present between Sun II and Garry and Rodney when he observed a quadrivalent in PMCs of the F_1 hybrids. The present results show that chromosomes 14 and 20 do not participate in this reciprocal translocation. The same conclusion can be extended to all the other chromosomes used in the crosses except chromosome 9 because the translocation was not present in the hybrids and ST-7 and ST-17 from A. byzantina.

Earlier work (Gauthier, 1967 and McGinnis, unpublished) has shown that the monosomics and nullisomics for chromosome 7 and 10 were characterized by curled leaves and kinky necks and those for chromosome 20 expressed only neck kinkyness. In addition, a haploid plant nullisomic for chromosome 7 (a different isolate than the one used in the present study) revealed a gene for diploidisation (Gauthier and McGinnis, 1968).

In the present study, Ditelosomic-20^L expressed only abaxial curling of the leaves. If the chromosomes previously identified as 7, 10 and 20 are in fact one and the same, it can be postulated that the gene(s) for normal leaves are located on the short

arm while the genes for diploidisation and normal neck shape are on the long arm of chromosome 20.

Meiotic behavior of ditelosomic-20^{L}.

Three aspects of the meiotic behavior were studied, namely the metaphase I pairing, the presence of micronuclei in tetrads and the somatic chromosome counts in the progeny.

The metaphase I pairing was studied by scoring the univalents and open and closed bivalents in 50 meiotic spreads. A disomic check was included for comparison. A very similar pairing behavior was observed in the ditelosomic line and the disomic check (Table 6). The average bivalent association was 20.96 and 20.98 for the ditelosomic and the disomic check, respectively. The presence of univalents was due to pairing failure of full univalents in either case. The minimum number of chiasmata was very similar, being 38.32 and 39.58 for the ditelosomic and disomic check, respectively, considering that the ditelosomic line has one less possible chiasma due to the open bivalent formed by the telocentric chromosomes.

In a sample of 1000 tetrads, ditelosomic-20^{L} produced 95.0% of n = 20 + t gametes while the disomic check produced 99.4% of normal gametes. The somatic chromosome counts of 70 seeds of ditelosomic-20^{L} revealed only ditelosomic plants.

(b) Ditelosomic for chromosome 21^{L}.

Two different isolates (Ditelo-102 and -105) were found to be ditelosomic for the long arm of chromosome 21 (Plate 3) by karyotype analysis.

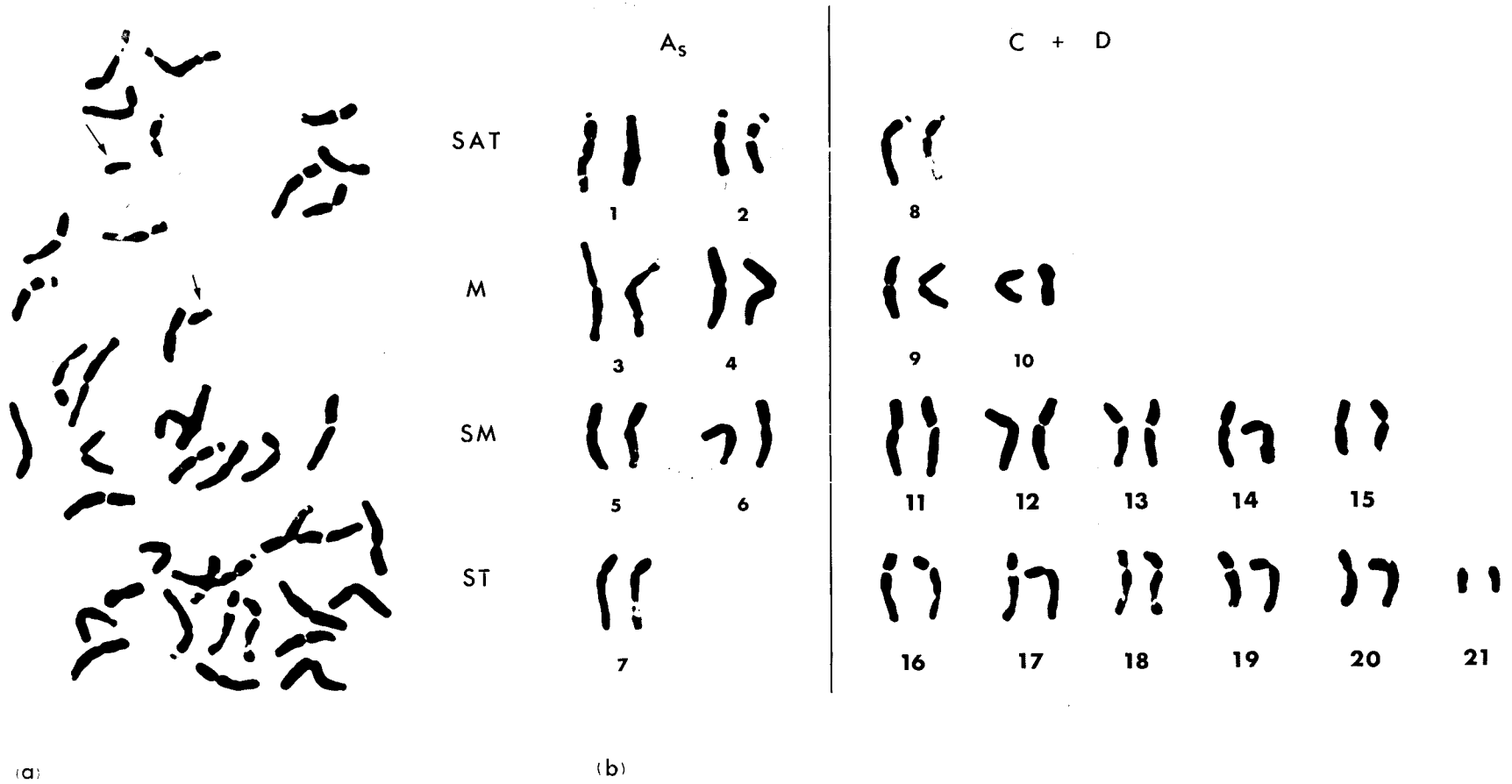
Table 6. Metaphase I pairing studies.

Line	Cells scored	Bivalents Univ. (range)	Open (range)	Closed (range)	Average Biv. assoc.	X-asma (range)
Ditelosomic for 20^L	50	.08 (0 - 2)	3.60 (1 - 7)	17.36 (20 - 14)	20.96	38.32 (35 - 41)
Ditelosomic for 21^L	50	.04 (0 - 2)	3.88 (1 - 8)	17.10 (20 - 13)	20.98	38.08 (34 - 41)
Disomic check	50	.04 (0 - 2)	2.38 (0 - 10)	18.60 (21 - 11)	20.98	39.58 (32 - 42)

Plate 3. Karyotype of ditelosomic 21^{L}.

a. Mitotic metaphase spread.

b. Karyotype analysis of a.


A$_S$
C + D
SAT
M
SM
ST
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
(a)
(b)

The meiotic behavior of ditelosomic-21^{L} (isolate ditelo-105) was very similar to the disomic check, the average bivalent association being 20.98 for both of them (Table 6).

(c) Other ditelosomic lines studied.

Three ditelosomic lines (Ditelo-3, -21 and -101) were found to be ditelocentric for the same chromosome arm when crossed to each other (Table 4). The F_1 40 + 2t-chromosome hybrids showed a pairing of 20 bivalents plus an open bivalent involving the two telocentrics. The telocentric chromosome in these three ditelosomic lines is involved in the reciprocal translocation present between the variety Sun II and Garry and Rodney. These ditelosomic lines proved to be deficient for an arm of a chromosome other than 1, 2, 4, 6, ST-7, 8, 9, 12, 13, 14, 15, ST-17, 18, 20 and 21.

Gx - 240, a line with a homozygous deletion for a part of a small arm, was found to be deficient for a chromosome other than 1, 2, 8, 9, 13, 20 and 21 by phenotypic, karyotype and cytological analyses.

(3) Study of somatic association of homologous chromosomes.

The frequency distribution for non-homologous chromosomes (Fig. 2D) was not significantly different from that expected for a random distribution ($P > .05$). The mean and variance were 0.430 and 0.018, respectively. The close fit to the theoretical curve verifies the assumption that the non-homologous chromosomes were distributed at random in the flattened cell.

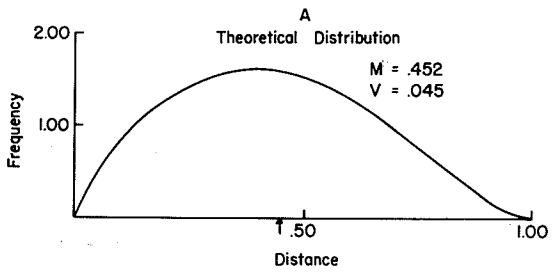
The homologous chromosomes were not distributed at random (Fig. 2, B and C). The frequency distributions obtained for the telocentrics (Fig. 2C) and the pair of chromosome 21 (Fig. 2B) were skewed to the right, resulting in a lower mean value. The mean and variance were 0.368 and 0.047 and 0.389 and 0.048, respectively, for the homologues of chromosome 21 and the telocentrics. The frequency distributions for homologues were significantly different from the frequency distribution for non-homologous chromosomes($P < .05$). Furthermore, the frequency distribution for homologous chromosomes 21 did not differ significantly from the frequency distribution of the pair of telocentrics.

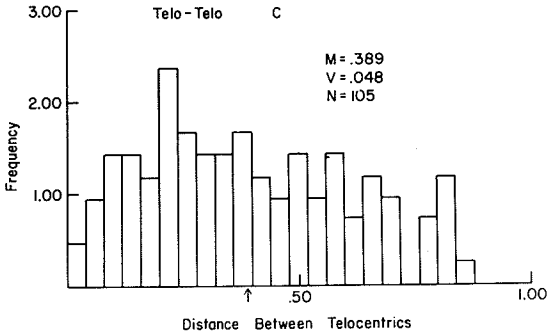
Figure 2. Frequency distributions of distances.

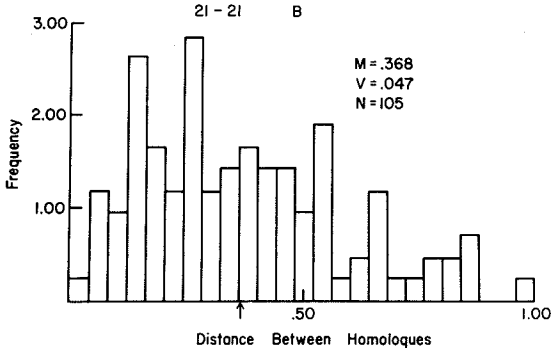
A. Between 2 points distributed at random in a circle.

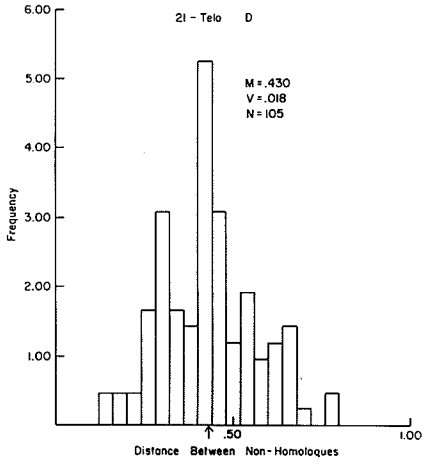
B and C. Between homologues 21 and homologous telocentrics, respectively.

D. Between non-homologous chromosome 21 and telocentric.


A
Theoretical Distribution
M = .452
V = .045
2.00
1.00
Frequency
.50
1.00
Distance


3.00
Telo - Telo C
M = .389
V = .048
N = 105
2.00
1.00
Frequency
.50
1.00
Distance Between Telocentrics


3.00
21 - 21 B
M = .368
V = .047
N = 105
2.00
1.00
Frequency
.50
1.00
Distance Between Homologues


6.00
21 - Telo D
5.00
M = .430
V = .018
N = 105
4.00
3.00
2.00
1.00
Frequency
.50
1.00
Distance Between Non-Homologues

GENERAL DISCUSSION AND CONCLUSIONS

Several methods have been used to identify the univalent chromosome in monosomic lines of common oats, namely phenotypic expression, karyotype analysis, chromosome arm ratio, transmission frequencies and interline crosses. Due to the nature of polyploids, several chromosomes are expected to control similar functions or have a similar arm ratio and transmission frequencies. Thus, McGinnis (1966) concluded that the only reliable monosomic identification method was by cytological analysis of interline hybrids coupled with karyotype analysis.

The production of interline hybrids and their cytological analysis are not without difficulties. The production of interline hybrids is hindered by negative certation effect and non-viability of the 20-chromosome pollen. The value of cytological analysis of F_1 40-chromosome hybrids is degraded by the small number of hybrid plants available, the possibility of univalent shift and selfing, and the possible misinterpretation of the data when different species of Avena are used due to the presence of univalents and multivalents.

The use of ditelosomic lines would overcome many of the problems. Cytological analysis are performed on F_1 40 + t-chromosome hybrids. They are obtained by fertilisation of a 20-chromosome gamete with a 20 + t-chromosome pollen grain. Theoretically, ditelosomic lines produce only 20 + t-chromosome pollen, thus eliminating the problems with certation effect and non-viability of the desired type of pollen. The efficiency in crosses is increased tremendously, the majority of the hybrids obtained being 40 + t-chromosome. The problem of undetected selfing is non existent because the hybrids are selected on the basis

of somatic chromosome number and the presence of the telocentric serves as a marker to identify the source of the pollen. The chance of univalent shift giving rise to erroneous conclusions is almost eliminated by studying more than one F_1 hybrid.

Ditelosomic lines have been used in this study to verify monosomic identification and to determine the presence of somatic association of homologues in common oats.

Gauthier (1967) made an interline cross between monosomic 7 and 20, the meiotic pairing study of the hybrids showed 19 bivalents plus 2 univalents indicating that the lines were deficient for two different chromosomes. In this study the same monosomic lines and a monosomic for chromosome 10 were crossed to a ditelosomic line for chromosome 20^L, the meiotic metaphase I pairing showed a telocentric univalent and 40 chromosomes involved in associations in all three cases. It was then concluded, that the three previously identified lines monosomic for chromosome 7, 10 and 20 were deficient for the same chromosome, namely 20. The results obtained by Gauthier can be explained by univalent shift because he found three double monosomic plants in the self progeny of monosomics 7 and 20. The use of a ditelosomic line in this case proved to be successful in detecting misidentification. There is no doubt that ditelosomics will contribute more in future cytogenetic studies.

Interline crosses between monosomic lines will have to be used for chromosome identification until a complete ditelosomic series is established in Avena. Presently, there are only 2 ditelosomic lines identified, namely 20^L and 21^L and two more are being studied, namely 14^S and 15^S.

Ditelosomic lines were also used to associate genes with specific

arms of chromosomes and to identify chromosomes involved in reciprocal translocation. A successful association of genes for normal leaf shape and for diploidisation was made with chromosome 20^S and 20^L, respectively. The chromosomes involved in the reciprocal translocation between the variety Sun II and Garry and Rodney were not identified positively but many possibilities have been eliminated.

The phenomenon of somatic association of homologous chromosomes has been shown to be present in certain species of animals and plants. Ditelosomic plants are ideal for the study of the phenomenon in Avena because they provide a clearly identifiable chromosome pair. The distances between homologous and non-homologous chromosomes were measured and the frequency distributions were compared. Association of homologues was detected because they tended to lie closer to each other than would be expected by chance alone. On the other hand, non-homologous chromosomes were distributed at random in the cell. Thus, it is concluded that somatic association which affects the spatial distribution of homologues is present in Avena.

It is interesting to note that a diploidisation gene was discovered in Avena (Gauthier and McGinnis, 1968). In wheat, a similar gene influenced the spatial distribution of the chromosomes by acting as a suppressor of somatic association. In its absence, the homoeologous chromosomes paired to form multivalents. The diploidisation gene may have a similar role in Avena but this is yet to be demonstrated.

A study of somatic association in nullisomics for the chromosome carrying the diploidisation gene would be appropriate but the chromosome carrying the function is involved in a translocation (Gauthier and McGinnis, 1968). It is not known if the gene is carried on the trans-

located segment because the results were obtained on a nulli-haploid plant. The translocated chromosomes will have to be identified in this monosomic line before the role of the diploidisation gene on somatic association is determined.

CONTRIBUTION TO KNOWLEDGE

1° A ditelosomic line for 20^{L} was identified and studied meiotically. The gene for normal neck shape was confirmed to be on 20^{L}. The genes for normal leaf shape and for diploidisation were associated with the short and long arm of chromosome 20, respectively.

2° Lines previously identified as monosomic for chromosome 7, 10 and 20 were found to be deficient for the same chromosome, namely 20.

3° Two different isolates were shown to be ditelosomic for 21^{L} by karyotype analyses.

4° The chromosomes involved in the reciprocal translocation between the variety Sun II and Garry and Rodney were found to be different than 4, 6, 12, 14, 15, 18, and 20.

5° Three different isolates (Ditelo-3, -21 and -101) were found ditelosomic for the same chromosome arm. The chromosome involved proved to be different from 1, 2, 4, 6, 8, 9, 12, 13, 14, 15, 18, 20, and 21 by phenotypic, karyotypic and cytological analyses.

6° The monosomic lines R - 127 and Gx - 164 were identified as monosomic 6 and 10, respectively by cytological analyses.

7° Two isolates (Mono $^{8}/1$ and Mono $^{8}/2$) nullisomic for chromosome 15 were identified by cytological analyses.

8° Two monosomic lines Gx - 99 and Gx - 154 were shown to be deficient for chromosome 21 by karyotype analyses.

9° The unidentified monosomic lines Gx - 26, Gx - 58, Gx - 69, Gx - 438, Gx - 623 were shown to be deficient for a chromosome other than those listed in table 5.

10° A somatic association of homologous chromosomes was found to be present in the species.

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APPENDIX (definitions)

Aneuploid line: A line whose somatic nuclei do not contain an exact multiple of the haploid number of chromosomes.

Asynapsis: The failure of homologous chromosomes to pair during meiosis.

Desynapsis: The falling apart during diplotene of meiosis of chromosomes which paired normally at pachytene.

Fatuoid line: A line characterized by a fatuoid phenotype, i.e., geniculate awn on each floret and a pubescent sucker mouth attachment to the rachilla.

Monosome: A monosomic chromosome.

Monosomic chromosome: A chromosome in the chromosome complement lacking an homologous partner.

Monosomic line: A line in which all the individuals lack one member of one particular pair of chromosomes.

Monosomic series: A series of all possible monosomic lines.

Nullisomy: The condition of an individual with both members of one particular pair of homologous chromosomes missing from the chromosome complement.

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