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A study of homoeologous relationships in the cultivated oat *Avena sativa* (2n = 6x = 42)

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Summary. The homoeologous relationship of the chromosomes of the allopolyploid species *Avena sativa* has been demonstrated by studies of nullisomic-tetrasomic compensation. The effects of the deletion of chromosome VI was partially compensated for by a tetrasomic dose of chromosome XIII, both at the gametic and zygotic level. The data confirm the genetic similarities of the homoeologues, which are attributable to their evolutionary derivation from a common chromosome.

Key words: *A. sativa* – Nullisomic – Tetrasomic compensation

Introduction

The cultivated oat *Avena sativa* (2n = 6x = 42) is a natural allopolyploid combining three distinct diploid genomes A, C and D (Rajhathy and Morrison 1960). On account of the genetic duplication inherent in such a polyploid structure, aneuploidy in the form of a deletion (monosomy) or duplication (trisomy) is readily tolerated (McGinnis 1966; Hacker and Riley 1965; Rajhathy and Thomas 1974). However, the loss of a pair of chromosomes (nullisomy) has a variable effect depending on the chromosome deleted. The absence of some chromosome pairs has a deleterious effect, the nullisomic plants being weak and sterile, while the loss of other chromosomes has little effect and the nullisomics are both vigorous and fertile.

Since *A. sativa* is a hexaploid species incorporating three diploid genomes it is reasonable to assume that genetically equivalent pairs of chromosomes (homoeologues) occur in each of the three constituent genomes. The genetic similarity of the homoeologues would be a reflection of their evolutionary derivation from a common chromosome. McGinnis (1966) proposed that the three chromosomes on which genes controlling chlorophyll synthesis are located probably constitute such a homoeologous group. Similarly McKenzie et al. (1970) speculated that, since genes controlling seedling resistance to stem rust could be classified into three independent linkage groups, the three chromosomes concerned could constitute a homoeologous group. Moreover Thomas and Bhatti (1975) and Azael (1974) have demonstrated nullisomic-tetrasomic compensation in *A. sativa* which provides unequivocal evidence of similarities in gene sequences in homoeologous chromosomes.

In this paper we report studies of nullisomic-tetrasomic compensation using the tetrasomic line for the shortest chromosome of the complement, XIII or ST21 according to Rajhathy's (1963) standard karyotype.

Materials and methods

The monosomic lines and the tetrasomic XIII line used were isolated in the cultivar 'Sun II'. Only fifteen of the monosomic lines (I–XV) were available.

The monosomic plants were each used as the female parent in crosses with the tetrasomic line and plants with 42 chromosomes identified as seedlings. At meiosis they formed $19^{II} + 1^{III} + 1^{I}$. The chromosome number of F_2 populations from each cross, except the Mono V and VII crosses, was determined and the number of ST21 chromosomes present recorded. ST21 is the shortest sub-terminal chromosome of the complement and its presence can be unequivocally identified in all dividing cells. The plants were grown in 5″ pots in the glasshouse.

For studies of mitotic chromosomes the seedlings were germinated at 22 °C and root tips 10–20 mm long were pretreated in chilled distilled water (0–2 °C) for 24 h. The root tips were fixed in 3 ethanol : 1 acetic acid solution and stained in Feulgen reagent after hydrolysis in normal HCl for 10 min at 60 °C. The stained root tips were squashed in 1% acetocarmine.

For meiotic studies immature panicles were fixed in Carnoy's fixative (6 ethanol : 3 chloroform : 1 acetic acid) to which a few drops of saturated solution of ferric chloride had been added. Anthers were stained in alcoholic hydrochloric acid carmine stain (Snow 1963) and squashed in 45% acetic acid.

Results

The mono-trisomic plants form four types of gametes $n=21^{I}$, $n+1=20^{I}+1^{II}$, $n-1=20^{I}$ and $n-1+1=19^{I}+1^{II}$. Mono VI plants yielded 0.05 euploid, 0.83 monosomic and 0.12 nullisomic progeny and Tri XIII gave 0.73 euploid, 0.25 trisomic and 0.02 tetrasomic progeny. Using the formulae of Hacker (1965) it is possible to calculate the frequency of functioning euploid and aneuploid eggs and pollen in the monosomic and trisomic lines. Assuming that the transmission of the monosome and trisome in the mono-trisomic F_1 hybrids is comparable to their transmission in the respective monosomic and trisomic parent plants, the proportion of the four types of gametes produced that will function in fertilization is calculated. Using these calculated frequencies it is then possible to calculate the expected frequencies of the different genotypes in the F_2 population.

On selfing the mono-trisomic plants nine genotypes combining the variable aneuploid state of the monosome and trisome are possible. In the present study the positive identification of the ST21 chromosome makes it possible to classify the progeny into the expected 9 classes, but in this study interest focuses only on the nulli-trisomics and nulli-tetrasomics. No nulli-tetrasomic plants were recovered from any of the F_2 families from the different mono-trisomics. The number of nulli-trisomics recorded and the calculated expected frequencies are presented in Table 1.

In general $n-1$ and $n+1$ pollen are at a selective disadvantage compared with haploid pollen and only participate in fertilization at a low frequency, hence the low number of nullisomic and tetrasomic progeny recovered from selfing monosomics and trisomics respectively. The number of chromosomes is restored to the haploid number in $n-1+1$ pollen but it carries a deletion and duplication. In wheat Sears (1966) has demonstrated that if the extra chromosome is of the same homoeologous group as the deleted chromosome the pollen will compete more effectively with haploid pollen than the $n-1$ pollen. The presence of the extra dose of the trisome compensates for the loss of its homoeologue at the gametic level and should increase the frequency of nulli-trisomic and nulli-tetrasomic progeny from selfing monotrisomic plants.

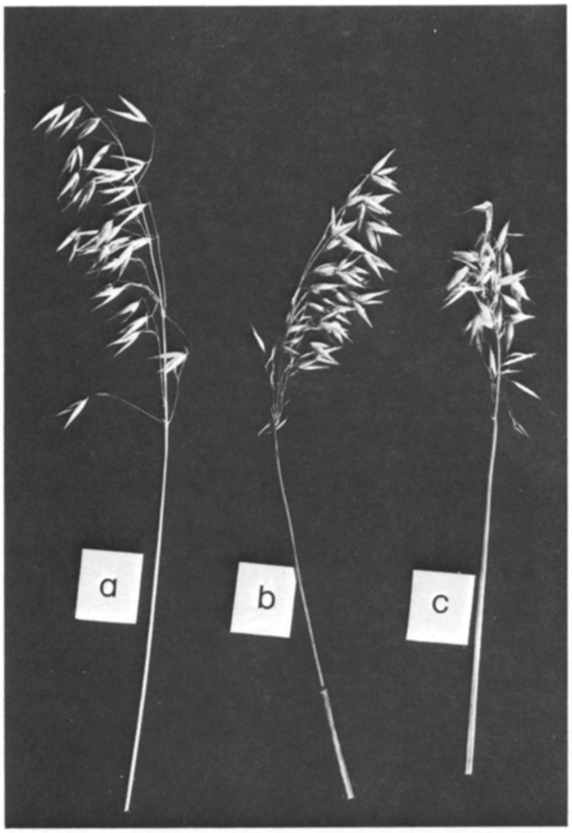

Fig. 1. Panicles of **a** 'Sun II', **b** nullisomic VI – tetrasomic XIII and **c** nullisomic VI

Only in hybrids involving mono-, II, III and VI were nulli-trisomic plants isolated. The nulli-trisomics were grown to maturity and those isolated from Mono II and III hybrids were identical to their respective nullisomics and were self-sterile. There was no evidence of nullisomic-tetrasomic compensation at the zygotic level in either line. However, the nulli-VI/trisomic XIII plants were more vigorous than nullisomic VI and were

Table 1. The number of nulli-trisomic progeny in F_2 populations from different mono-trisomics

	Monosomic											
	I	II	III	IV	VI	VIII	IX	X	XI	XII	XIV	XV
Observed	0	2	1	0	4	0	0	0	0	0	0	0
Expected	1.44	0.9	2.6	0.5	1.1	0.02	0.09	0	0.09	0	0	0
No. of plants scored	24	13	26	18	37	35	30	49	32	55	25	18

Table 2. Comparison of nullisomic VI and nullisomic VI-tetrasomic XIII for panicle size and seed setting

	Length of panicle (cm)	No. of spikelets	No. of seeds
Nullisomic VI	11	16	0
Nullisomic VI-tetrasomic XIII	17	57	37

partly fertile compared with the self-sterility of nullisomic VI.

A comparison of panicle characteristics of the nullisomic and nulli-tetrasomic genotypes is presented in Table 2. The nulli-tetrasomic plants were obtained from selfing the nulli-trisomics which yielded 31% nulli-tetrasomic progeny. The panicle of the nullisomic VI plants is much reduced compared with euploid Sun II plants and it has a characteristic blasting (abortive flowers) of the lower spikelets (Plate 1). The panicle of nulli-VI/tetrasomic XIII is larger than nullisomic VI but the blasting of the lower spikelets is still prevalent. Fertility is partially recovered in the nulli-tetrasomic but is much lower than the euploid. The nulli-tetrasomic plants were equal in height to the euploid but had less tillers.

Discussion

The morphology and fertility of the nullisomic VI/tetrasomic XIII plants clearly show that the extra dose of chromosome XIII partially compensates for the deletion of chromosome VI. However, the characteristic blasting of the lower spikelets in the panicles of nullisomic VI plants was also present in the nulli-tetrasomic and the tetrasomic condition of chromosome XIII did not compensate for this irregularity, which is attributed to the deletion of chromosome VI. There was no evidence of nullisomic-tetrasomic compensation in any of the lines other than VI.

The extent of compensation recorded at the gametic and zygotic level indicates that chromosomes VI and XIII are homoeologous. Karyotype analysis showed that chromosome VI is the same as M4 in Rajhathy's (1963) designations and chromosome XIII is ST21. McGinnis (1966) proposed that chromosomes M4, ST21 and SM15 probably constituted a homoeologous group on account of these chromosomes being associated with chlorophyll synthesis. The data presented confirm that ST21 (XIII) and M4 (VI) are homoeologous.

The present study together with the previous studies by Thomas and Bhatti (1975) and Azael (1974) show conclusively the occurrence of nullisomic-tetrasomic compensation in *A. sativa*. The ability of homoeologous chromosomes to compensate for one another is due to similar gene sequences probably arising from their evolutionary derivation from a common chromosome. The chromosomes of *A. sativa* probably fall into seven homoeologous groups as in *Triticum aestivum* (Sears 1966).

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References

Azael A (1974) Die Homoeologie der Chromosomen 2, 15 und 21 von Hafer, *Avena sativa* L. Z Pflanzenzücht 71:12–24

Hacker JB (1965) The inheritance of chromosome deficiency in *Avena sativa* monosomics. Can J Genet Cytol 7:316–327

Hacker B, Riley R (1965) Morphological and cytological effects of chromosome deficiency in *Avena sativa*. Can J Genet Cytol 7:304–315

McGinnis RC (1966) Establishing a monosomic series in *Avena sativa* L. In: Riley R, Lewis KR (eds) Chromosome manipulations and plant genetics. Oliver and Boyd, Edinburgh, pp 296–301

McKenzie RH, Martens JW, Rajhathy T (1970) Inheritance of oat stem rust resistance in a Tunisian strain of *Avena sterilis*. Can J Genet Cytol 12:501–505

Rajhathy T (1963) A standard karyotype for *Avena sativa*. Can J Genet Cytol 5:127–132

Rajhathy T, Morrison JW (1960) Genome homology in *Avena*. Can J Genet Cytol 2:278–285

Rajhathy T, Thomas H (1974) Cytogenetics of oats (*Avena* L.). Misc Publ Genet Soc Canada 2:1–91

Sears ER (1966) Nullisomic-tetrasomic combinations in hexaploid wheat. In: Riley R, Lewis KR (eds) Chromosome manipulations and plant genetics. Oliver and Boyd, Edinburgh, pp 29–45

Snow R (1963) Alcoholic hydrochloric acid-carmine as a stain for chromosomes in squash preparations. Stain Technol 38:9–13

Thomas H, Bhatti IM (1975) Notes on the cytogenetic structure of the cultivated oat *Avena sativa* ($2n = 6x = 42$). Euphytica 24:149–157