NOTES AND COMMENTS

CHROMOSOME REARRANGEMENTS IN THE HEXAPLOID OATS

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1. Introduction

The hexaploid oats constitute an extraordinarily variable complex of wild weedy and cultivated plants. This complex is usually divided by botanists into three main morphological types. The wild and weedy forms in which the florets of each spikelet fall jointly at maturity are referred to as *Avena sterilis* L. weed forms in which each floret falls separately to serve as an independent diaspor, are identified as *A. fatua* L. Non-shattering, cultivated forms are grouped as *A. sativa* L. and *A. byzantina* C. Koch. But all are interfertile and hybrids between the main types show full chromosome pairing in meiosis. Furthermore, in the belt of Old World Mediterranean Agriculture, the various tame and wild forms grow side by side and are genetically interconnected by spontaneous hybridisation and subsequent gene-flow.

A conspicuous feature of the hexaploid oats is their pronounced weedy habit and colonising ability. Both *sterilis* and *fatua* oats are among the most successful colonising plants in the belt of Mediterranean Agriculture. They massively occupy opened up areas and agricultural lands from the Atlantic coast to Iran. They successfully penetrate as weeds in cereal fields far into northern Europe. Also, the distribution of the cultivated varieties is apparently closely linked with that of their weedy forms. Oats are one of Vavilov's classical examples of " secondary crops ".

Some basic elements of the genetic system operating in these colonising oats are well understood. Polyploidy is an essential element. As in the weedy *Aegilops* (Zohary, 1965), polyploid *Avenae* are successful weeds while the diploid *Avena* species are more specific in their ecological requirements. Polyploid oats are also characterised by diploidisation of their chromosome system: although interspecific hybrids between the diploid *Avena* species show a considerable amount of chromosome pairing in meiosis there is practically no multivalent formation either in tetraploid or hexaploid oats. Finally, oats are predominantly self-pollinating, though both cultivated and wild hexaploids maintain some percentage of cross-pollination. Thus, different types growing sympatrically occasionally cross with one another. Such genetic links have been demonstrated in polymorphic wild populations (Imam and Allard, 1965).

The present paper aims at focusing attention on another feature which apparently characterises the genetic system of the variable hexaploid oats, namely intragroup, chromosomal variation. That different varieties of cultivated *A. sativa* differ from one another chromosomally is apparent from the karyomorphological comparison of cultivars " Markton " and " Condor" drawn by Marenah and Holden (1967). Oat breeders (H. C. Murphy, personal communication) have encountered formation of translocation quadrivalents in several *sativa* × *sativa* or *sativa* × *sterilis* hybrids. In the present paper, further information on chromosome variation in hexaploid oats is presented, and its significance in the enhancement of variation in this group of plants is discussed.

2. Methods

Chromosomal variation was examined by a comparison of meiosis behaviour between parental lines and their hybrids. Anthers were fixed in 3 : 1 alcohol-acetic acid for 24 hours, stored in 70 per cent. alcohol and stained in acetocarmine.

Pollen fertility was determined by dissecting mature anthers, soaking them in 2 per cent. aceotcarmine and scoring about 500 grains per plant. Seed fertility was determined by examination of the two lower florets of the spikelet. A floret was considered fertile if it produced a well-developed kernel. In both parental lines and hybrids, 100 florets were examined in each plant.

3. Results

Six different hybrid combinations involving six *sterilis* lines and a single *byzantina* line were employed. These lines represent different ecogeographical races (table 1).

Table 1

Parental lines used in crosses

Accession No.		Source
6510	*A. sterilis*	Israel, Jerusalem. Dwarf shrub formation. Terra-rossa soil.
6511	*A. sterilis*	Israel, Rehovot. Edges of cultivation. Sandy loam soil.
6512	*A. sterilis*	Israel, 10 km. N. of Tiberias. Herbaceous formation, basaltic hill.
6513	*A. sterilis*	Israel, 15 km. N.W. of Beer-Sheva steppe, Loess soil.
6514	*A. byzantina*	Cultivar Mulga.
6517	*A. sterilis*	Turkey, Manisa, edges of vineyards. Alluvial soil.
6518	*A. sterilis*	Turkey, Gaziantep. Edges of plantation. Terra-rossa soil.

Meiosis in parental lines. Six of the parents ($2n = 42$) showed normal formation of 21 bivalents in meiosis. One parent (6510) was exceptional, it had $2n = 43$ chromosomes and showed typical trisomic behaviour in Metaphase 1 (table 2). Pollen fertility and seed set were normal in all seven parents, including the trisomic plant (table 2).

Meiosis in the F_1 hybrids. All six hybrid combinations examined were characterised by formation of 1 or 2 quadrivalents (table 2). In two hybrids (6514 × 6510 and 6511 × 6513) conspicuously heteromorphic quadrivalents were detected, indicating that the lines involved differed from each other by unequal reciprocal translocation. Also, the frequency of formation of quadrivalents (and trivalents) differed from hybrid to hybrid, indicating

TABLE 2

Cytology and fertility of parental lines and their hybrids in the hexaploid oats

	No. of cells examined	Univalents	Bivalents	Trivalents	Quadrivalents	Pentavalents	Mean chiasmeta per cell	% pollen fertility	% seed set
Parental lines									
*6510	20	0·5 (0-1)	20·5 (20-21)	0·5 (0-1)			43·40 ± 2·44	99·6	100
6511	20		21				45·27 ± 2·09	93·2	100
6512	20		21				47·55 ± 0·90	96·4	98
6513	20		21				44·25 ± 0·90	99·6	100
6514	20		21				42·15 ± 2·85	94·3	100
6517	20		21				42·15 ± 2·11	94·1	100
6518	20		21				42·15 ± 1·56	99·5	100
F_1 Hybrids									
**6514 × 6510	48	1·50 (0-5)	18·30 (15-21)	0·82 (0-3)	0·24 (0-2)	0·04 (0-1)	38·14 ± 2·43	84·6	100
6510 × 6511	48	0·58 (0-3)	19·64 (19-21)	0·29 (0-1)	0·31 (0-1)		38·31 ± 1·98	91·9	100
6518 × 6510	30	0·13 (0-3)	20·61 (19-21)	— —	0·16 (0-1)		40·53 ± 2·33	89·7	97
6517 × 6513	48	0·26 (0-2)	19·63 (17-21)	0·43 (0-2)	0·03 (0-1)		36·25 ± 2·71	95·2	100
6512 × 6510	30	0·16 (0-2)	20·73 (19-21)	0·03 (0-1)	0·06 (0-1)		39·96 ± 1·91	79·9	100
**6511 × 6513	48	1·50 (0-4)	18·13 (15-20)	0·85 (0-3)	0·40 (0-2)	0·02 (0-1)	36·95 ± 1·98	92·5	100

* This parent was trisomic (2n = 43). ** This hybrid showed a heteromorphic quadrivalent.

that exchanges were not identical. The trivalents and most of the quadrivalents were of the chain type though only a few of the latter were ring or ring-chain types. In two hybrids an occasional pentavalent was also observed. But in spite of the multivalent formation and the slight decrease in chiasma frequency, the fertility of the hybrids was not impaired. Pollen fertility was almost as good as in parental lines, and seed set was normal (table 2).

4. Discussion

The results obtained indicate that multivalent configurations in the hybrids of the hexaploid oats are apparently common. These results are similar to those recently demonstrated in the tetraploid oats *A. barbata* (Holden, 1966; Tabata and Nishiyama, 1966; Ladizinsky and Zohary, 1968).

Multivalent formation in the hybrids of the polyploid oats could be the results of two different sources. Homoeologous pairing due to partial breakdown of the diploidisation mechanism, and chromosome rearrangements in the different lines. The occurrence of heteromorphic configurations in several hybrid combinations strongly indicates that at least part of the multivalent formation is of the latter cause.

The question naturally arises as to what is the role of these chromosomal repatternings in the apparent and recent evolutionary success of the polyploid oats. The fact that all hybrids between the lines tested show normal seed set strongly indicates that hybridisation and gene-flow are effectively buffered by polyploidy. We are thus not faced here with the build up of sterility barriers between types. Rather than reflecting speciation and enforcement of reproductive isolation, the chromosomal variation encountered could indicate genetic polymorphism. In polyploids with diploidised chromosome behaviour in meiosis, and predominance of self-pollination, such chromosomal variation can be meaningful in terms of intergenomic gene interactions or intergenomic heterotic effects. Exchanges between chromosomes found in hexaploid oats can lead to repatterning of the genetic architecture and to fixation of new intergenomic heterotic effects. Translocations between homoeologous chromosomes is most likely a major contribution to the variation observed. As Riley and Kempanna (1963) have demonstrated, this type of recombination accounts for most of the non-homologous exchanges produced in hexaploid-wheat when the control of diploidisation (absence of chromosome 5B) is affected. But polyploidy in oats could effectively buffer also the presence of reciprocal translocations between non-related chromosomes of the three sets. Such exchanges might enhance linkage between favourable genes—near the breaking point.

The presence of considerable chromosome variation in *A. sterilis* and *A. byzantine* necessitates also a reconsideration of the karyomorphological work carried out in oats. Obviously if chromosome repatterning takes place, pitfalls must exist. Karyomorphological recognition of putative diploid ancestors becomes more hazardous, and comparison and identification of individual chromosomes—in different varieties—is sometimes impossible. These difficulties are well illustrated when the karyotype of cultivar, " Condor " (Marenah and Holden, 1967) is compared with the standard karyotype established by Rajhathy (1963) in cultivar, " Markton ".

5. Summary

1. Different lines of hexaploid oats (*A. sterilis-A. sativa* group) were found to differ from each other by chromosome rearrangements.

2. Five hybrid combinations between *A. sterilis* lines and one *sterilis-byzantina* combination were examined. All hybrids showed formation of 1-2 quadrivalents indicating translocation differences between lines.

3. These chromosomal differences did not affect the fertility of the hybrids, nor reproductively isolate the various forms.

4. It is proposed that chromosomal variation is an integral part of the genetic system of polyploid oats and one of the means enabling rapid evolution in the group of weeds and cultivated cereals.

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NOTES ON DR SNELL'S OBSERVATIONS CONCERNING THE H-2 *LOCUS* POLYMORPHISM

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1. Introduction

SNELL (1968) examined the possible adaptive significance of membrane polymorphism and compared viral oncogenesis, molecular mimicry, rate of virus penetration of cells depending on virus and host genotype, maternal-foetal interaction and heterozygous advantage and other possibilities as mechanisms which could maintain histocompatibility polymorphism and concludes that, theoretically, certain of these types of selection could function in this way while others could not.