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MEIOTIC STUDIES OF SOME *AVENA* SPECIES AND POPULATIONS IN IRAN

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Abstract

Eleven populations of five *Avena* species were analysed for meiotic characters including chiasma frequency and distribution as well as chromosomal association and segregation. Plants of a single population of *A. eriantha* showed the presence of 2n = 14 (diploid) and 2n = 4x = 28 chromosome number. Populations of *A. barbata* and *A. wiestii* possessed n = 14, while populations of *A. sterilis* ssp. *ludoviciana* possessed 2n = 6x = 42 (hexaploid) chromosome number. Tetraploid and hexaploid species showed diplontic behavior and formed only bivalents. The species and populations studied differed significantly in the frequency of chiasmata. B-chromosomes occurred in some of the species studied. Cytomixis and chromosome elimination led to aneuploid and unreduced pollen mother cell formation in the species studied.

Keywords: *Avena*; B-chromosomes; Chiasma frequency; Cytomixis

Introduction

The genus *Avena* L. (Tribe Aveneae) comprises about 27 species throughout the world [3], out of which 9 or 10 species occur in Iran [4,18]. These species are considered as important range grasses of Iran and grow wild throughout the country.

All *Avena* species are inbreeders and annuals with the exception of *A. macrostachya* Bal. ex Cosson & Dur. which is a perennial outbreeding species occurring in North Africa [19]. Although the available literature dealing with cytogenetics of *Avena* [for example: 1,2,8,12,14-16,19], indicate the importance of these taxa, no report is available on cytogenetics of *Avena* species and populations from Iran. Therefore the present study considers the meiotic analysis of some *Avena* species/populations in Iran trying to reveal the ploidy level and the basic cytogenetic information of these species for the first time.

Materials and Methods

Plant Material

Meiotic studies were performed on eleven populations of five *Avena* species, namely *A. eriantha* Dur., *A. barbata* Pott ex Link., *A. wiestii* Steud., *A. fatua* L., and *A. sterilis* ssp. *ludoviciana* L. (Table 1, Fig. 1). Voucher specimens are deposited in the Herbarium of Shahid Beheshti University (HSBU).

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Table 1. Chiasma frequency and chromosomes association in *Avena* species. Species and populations code : B1 & B2 = *A. barbata*, Dasht and Shiraz; F = *A. fatua* Esfahan; L1-L5 = *A. sterilis* ssp. *ludoviciana*, Varamin, Tehran-1, Tehran-2, Mahalat and Dasht respectively; W1 & W2 = *A. wiestii*, Gonbad and Tehran; E1 & E2 = *A. eriantha* Dasht

Sp	n	X	TX	IX	RDB	RB	TOX	U	TXB	IXB	TOB	RDN	RN
B1	14	4X	21.61	3.94	3.32	10.55	25.55	0.26	1.54	0.28	1.82	0.24	0.75
B2	14	4X	22.60	7.70	1.85	12.15	30.30	0.00	1.61	0.55	2.16	0.13	0.87
F	21	6X	30.31	8.69	4.69	16.08	39.00	0.46	1.44	0.41	1.85	0.22	0.76
L1	21	6X	32.26	7.16	3.26	17.37	39.42	0.74	1.54	0.34	1.18	0.15	0.83
L2	21	6X	35.43	8.38	2.52	18.48	43.81	0.00	1.69	0.40	2.09	0.12	0.88
L3	21	6X	26.71	4.00	8.88	11.71	30.71	0.82	1.27	0.19	1.46	0.42	0.55
L4	21	6X	36.53	9.00	1.47	19.47	45.53	0.12	1.74	0.43	2.17	0.07	0.93
L5	21	6X	35.00	5.55	3.97	16.97	40.55	0.14	1.66	0.26	1.92	0.19	0.80
W1	14	4X	21.29	6.43	4.14	9.86	27.71	0.00	1.52	0.46	1.98	0.29	0.70
W2	14	4X	23.45	6.25	2.33	11.68	29.70	0.00	1.67	0.45	2.12	0.17	0.83
E1	7	2X	8.73	3.27	1.64	5.18	12.00	0.36	1.25	0.47	1.72	0.26	0.74
E2	14	4X	24.81	5.09	0.54	13.46	29.90	0.00	1.72	0.36	2.13	0.04	0.96

Abbreviations: n = haploid chromosome number, X = ploidy level, TX= terminal chiasma, IX = intercalary chiasma, TOX = total chiasma, RB = ring bivalent, RDB = rod bivalent, U = univalent, TXB = terminal chiasma/ bivalent, IXB = intercalary chiasma/bivalent, TOB = total chiasma/bivalent, RN = ring bivalent/haploid chromosome number, RDN = rod bivalent/haploid chromosome number.

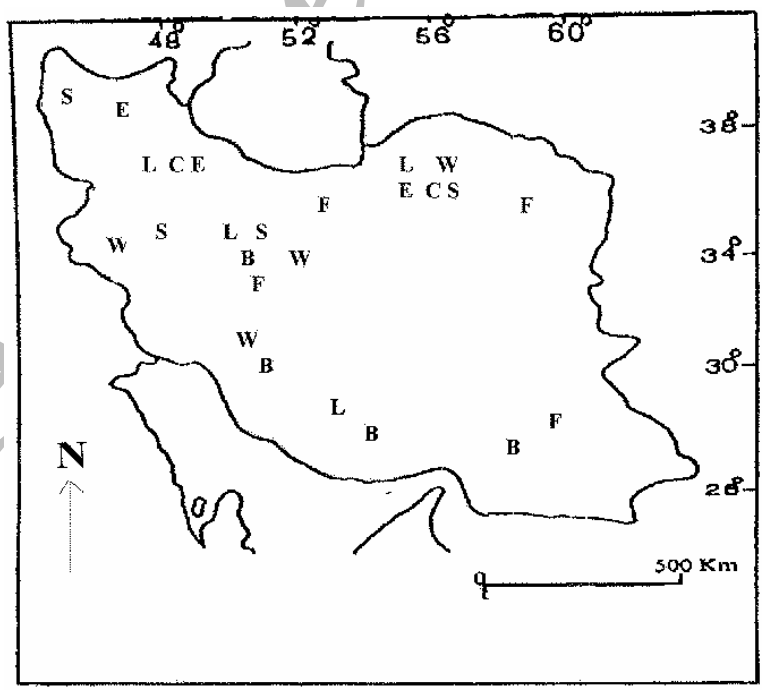

Figure 1. Distribution map of the *Avena* species. Abbreviations: B = *A. barbata*, E = *A. eriantha*, F = *A. fatua*, L = *A. sterilis* ssp. *ludoviciana*, W = *A. wiestii*.

Cytological Preparation and Meiotic Analysis

Young flower buds were collected from 10 randomly selected plants of each species/populations and fixed in glacial acetic acid: ethanol (1:3) for 24 h. Flower buds were then washed and preserved in 70% ethanol at 4°C until used [24,26] for cytological preparations, squash technique and 2% aceto-orcein (as the stain) were used.

Fifty to one hundred pollen mother cells (PMCs) were analysed for chiasma frequency and distribution at diakinesis/metaphase stage and 500 PMCs were analysed for chromosome segregation during the anaphase and telophase stages. Pollen stainability as a measure of fertility was determined by staining minimum 1000 pollen grains with 2% acetocarmine: 50% glycerin (1:1) for about ½ h. Round/ complete pollens which were stained were taken as fertile, while incomplete/shrunken pollens with no stain were considered as infertile [24,26].

In order to detect a significant difference in mean total and relative chiasma frequency and distribution as well as chromosomes association, t-test and analysis of variance (ANOVA) were performed between populations of a single species as well as among different species studied [24,26].

In order to indicate relation between pollen fertility and anaphase and telophase laggard chromosomes as well as pollen grains with extra chromosomes, Pearson coefficient of correlation was determined [24,26].

In order to group the *A. sterilis* ssp. *ludoviciana* populations having similar meiotic behavior, different methods of cluster analyses including single linkage, UPGMA and WARD as well as ordination based on principal components analysis (PCA) were performed [25] for multivariate statistical analyses, STATISTICA ver. 5 (1995) and SPSS ver. 9 (1998) softwares were used.

Results and Discussion

Chromosome Pairing and Chiasma Frequency

Data with regard to meiotic chromosome number, ploidy level, chiasma frequency and distribution, as well as chromosome pairing are presented in Table 1. (Fig. 2, a-v). Two populations of *A. barbata* possessed 2n = 28 chromosome number (4x, AABB) supporting the earlier reports [19,27].

A higher mean number of total, terminal and intercalary chiasmata as well as ring bivalent was observed in Shiraz population (B2 in Table 1) compared to that of Dasht population (B1). T-test analysis showed a significant difference between the two populations.

Although *A. barbata* is a tetraploid, it formed only bivalents in metaphase-I which is considered to be the cytogenetical characteristic of true allopolyploids. In fact it is a segmental allopolylploid having homoeologous chromosomes with a superimposed control of a diplodizing mechanism as suggested by Ladizinsky [14] and Rajhathy & Thomas [19].

A single population of *A. fatua* studied showed presence of 2n = 42 chromosome number (6x, AACCDD), supporting the earlier reports [19,27].

Two populations of *A. wiestii* studied showed the presence of *2*n = 28 chromosome number (4x). The earlier reports [8,19], considered *A. wiestii* as a diploid species (n = 7) with AsAs genome, however Baum in his monograph [3] considered it as a tetraploid species with no specific reference provided. Our literature review also did not show any record of n = 14 for *A. wiestii*, therefore according to our knowledge the present report of n = 14 (tetraploid level) is a new record.

Both populations of *A. wiestii* formed bivalents and univalents in metaphase of meiosis-I. Tehran population (W1) showed a little higher values for total and terminal chiasmata as well as ring bivalents compared to Golestan population (W2). T-test analysis showed a significant difference between the two populations.

Meiotic analysis of a single population of *A. eriantha* showed the presence of plants with two different chromosome numbers *i.e.*, 2n = 14 (2x) and 2n = 28 (4x). The earlier report [11] considered 2n = 14 (2x, CpCp) for *A. eriantha*, therefore 2n = 28 (4x) chromosome number is a new record for this species. In plants possessing 2n = 14 and 2n = 28 only bivalents were formed in metaphase-I.

ANOVA test performed separately on chiasma frequency and distribution as well as chromosomal association using mean total and relative values of meiotic data among *A. eriantha*, *A. barbata* and *A. wiestii* (all possessing n = 14 chromosomes number), showed a significant difference among the species studied. This may suggest that during diversification of these species the genes controlling chiasma frequency and distribution have changed significantly.

Five populations of *A. sterilis* ssp. *ludoviciana* possessed n = 21 (6x, AADDCC) chromosome number, supporting the previous report [12]. The populations studied showed a diplontic behavior and formed bivalents and univalents in metaphase of meiosis-I.

Among *ludoviciana* populations, Varamin (L4 in Table 1.) possessed the highest values for terminal, intercalary and total chiasma (36.53, 9.00 & 45.53 respectively), while Mahalat population (L3) possessed the lowest values for the same (26.71, 4.00 & 30.71,

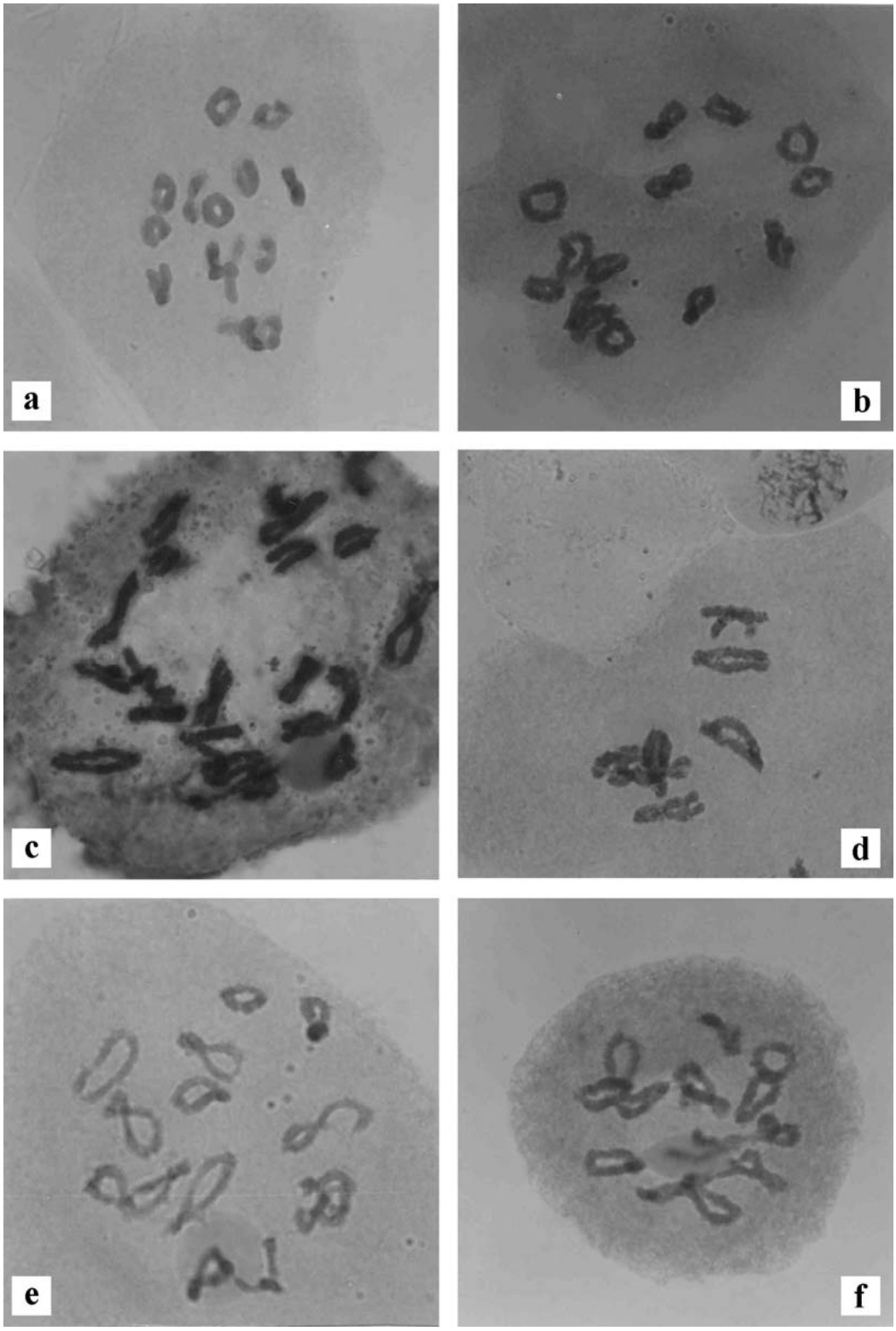

Figure 2. Representative meiotic cells in *Avena* species. **a** = *A. barbata* (Dasht population) showing n = 14; **b** = *A. wiestii* (Tochal population) showing n = 14; **c** = *A. fatua* (Esfahan population) showing n = 21; **d** = *A. eriantha* (Dasht population) showing n = 7; **e** = *A. barbata* (Shiraz population) showing n = 14; **f** = *A. eriantha* (Dasht population) showing n = 14.

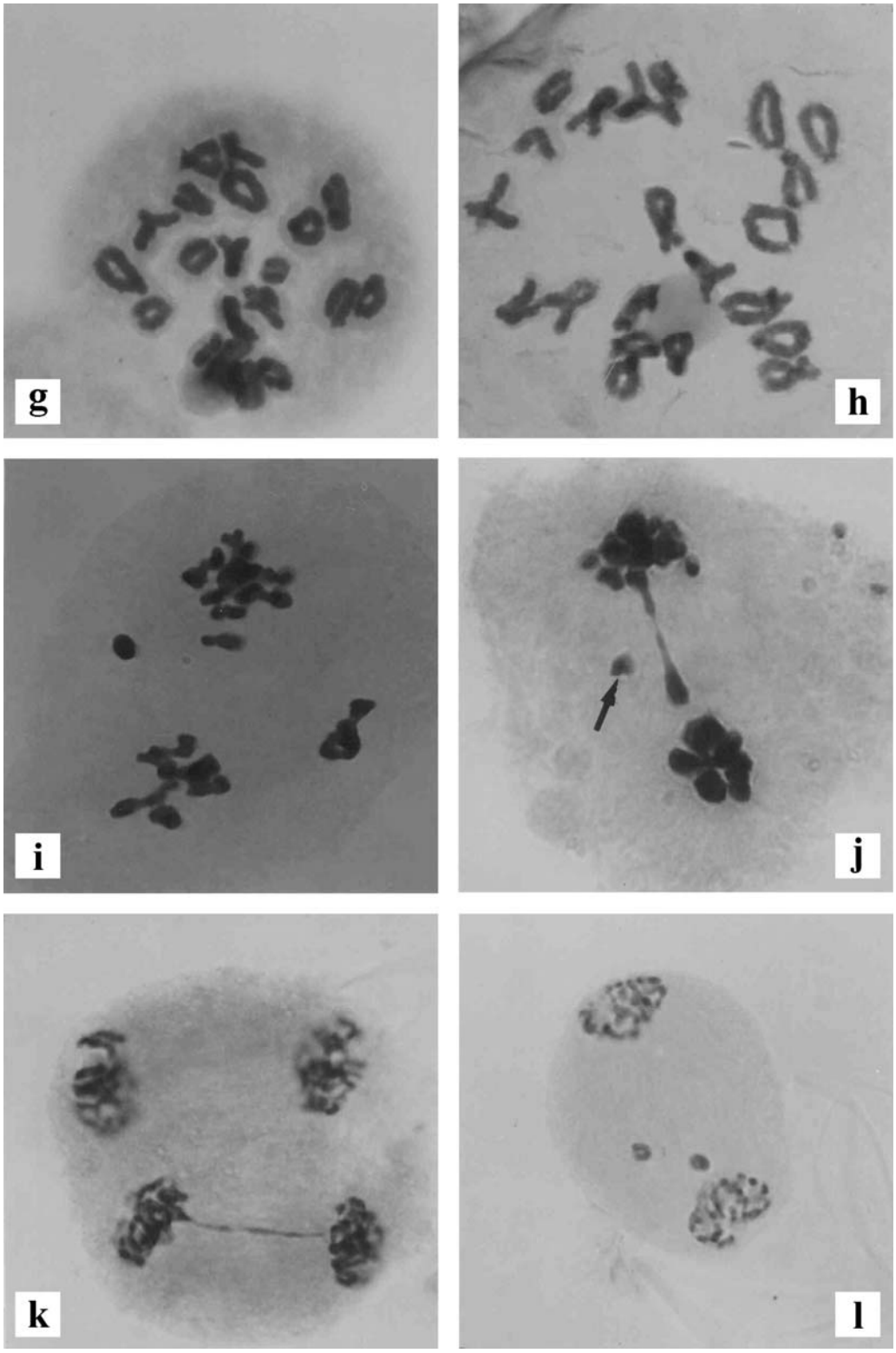

Figure 2. Representative meiotic cells in *Avena* species. **g** & **h** = *A. sterilis* ssp. *ludoviciana*, showing n = 21 in populations of Mahalat and Tehran respectively; **i** = multipolar cell in *A. barbata*; **j** = stickiness and laggard chromosome (arrow) in *A. sterilis* ssp. *ludoviciana*; **k** = stickiness in *A. barbata*; **l** = micronuclei in *A. wiestii*.

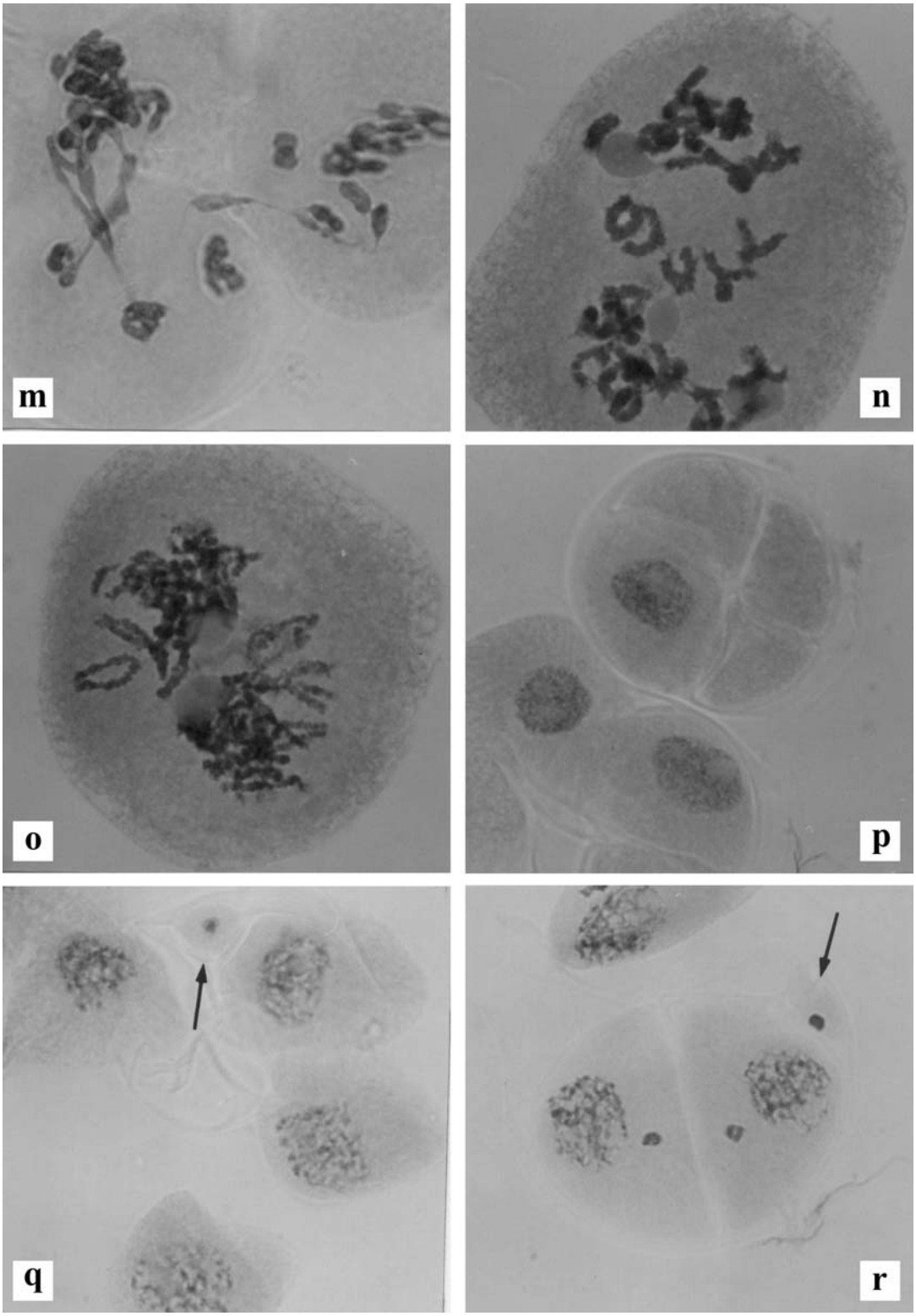

Figure 2. Representative meiotic cells in *Avena* species. **m** = chromosome migration in *A. wiestii*; **n** & **o** = cytomictic cells showing double chromosome number in *A. eriantha*; **p** = abnormal tetrad cells in *A. wiestii*; **q** & **r** = chromosome elimination in *A. wiestii* (arrow).

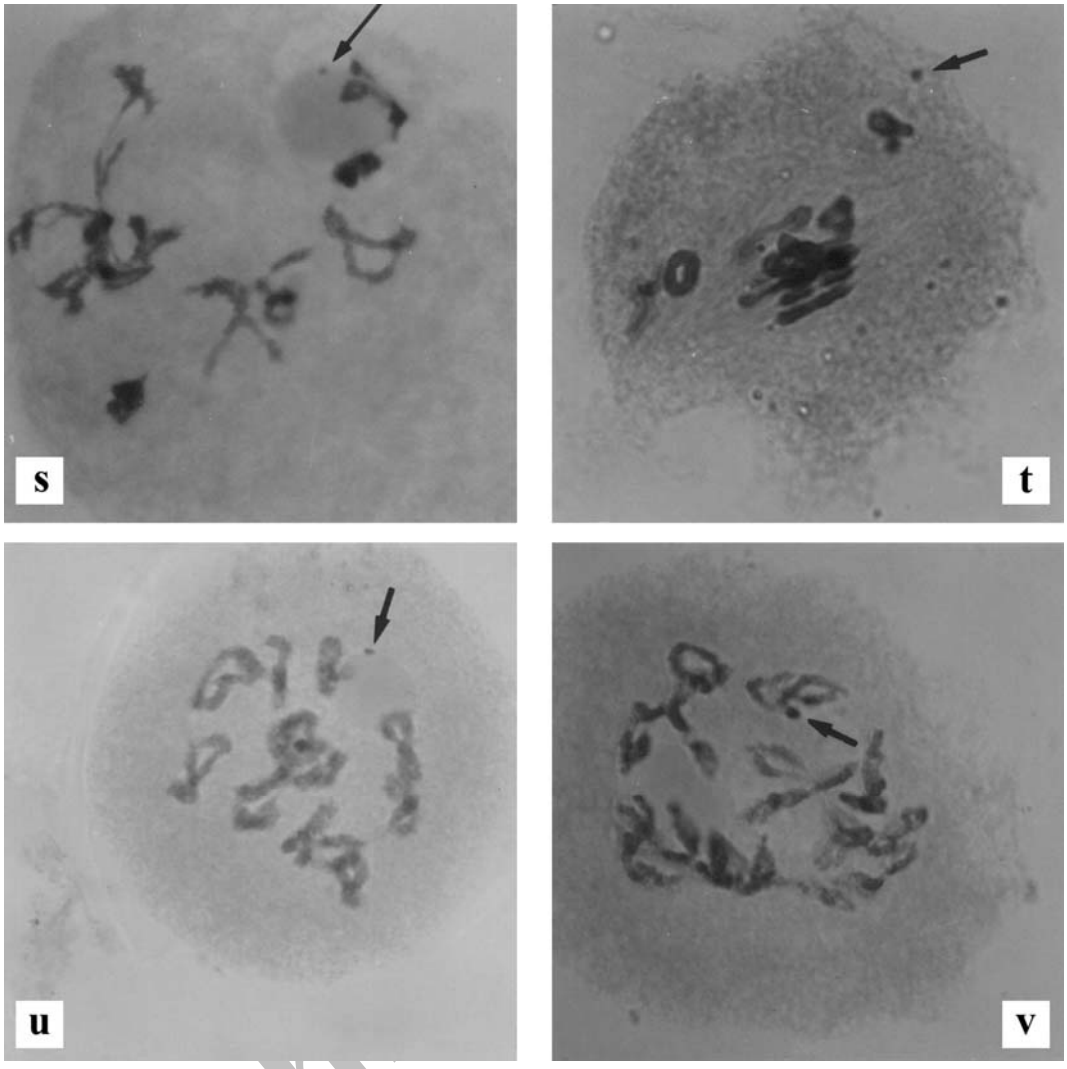

Figure 2. Representative meiotic cells in *Avena* species. **s** & **t** = B-chromosomes in *A. wiestii* (arrow); **u** = B-chromosomes in *A. barbata* (arrow); **v** = B-chromosomes in *A. eriantha* (arrow).

respectively). These two populations also showed the highest and the lowest values of ring bivalents (19.47 & 11.71 respectively). ANOVA test performed showed a significant difference in chiasma frequency and distribution as well as chromosomes association among these populations.

Different cluster analysis (single linkage, UPGMA and WARD) and ordination of the *A. sterilis* ssp. *ludoviciana* populations based on principal components analysis of meiotic characters produced similar results. Therefore only phenogram obtained from single linkage method is presented (Fig. 3), indicating that Mahalat population (L4) differs from the other populations as it stands in a separate cluster. It is interesting to mention that such variation is also observed in morphological characters [25].

ANOVA test performed on mean total chiasma frequency and distribution as well as chromosomes association between *A. sterilis* ssp. *ludoviciana* and *A. fatua* (both with n = 21), showed a significant difference between the two species.

Variation in chiasma frequency and localization is genetically controlled [6,10,14] and has been reported in populations of different grass species like *Aegilops*, *Lolium* and *Festuca* [21,24,26] as observed in the species/populations of *Avena*. Such a variation in the species/populations with the same chromosome number is considered as a means for generating new forms of recombination influencing the variability within natural populations in an adaptive way [20].

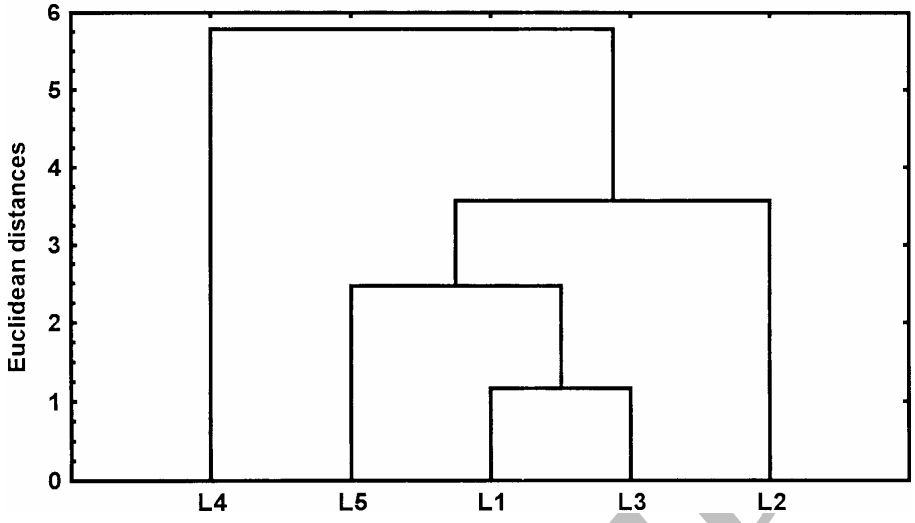

Figure 3. Cluster analysis (single linkage) of meiotic characters in *A. ludoviciana* populations. Species/populations code as in Table 1.

Table 2. Cells having laggard chromosomes and micronuclei (species code as Table 1)

Species	A1%	A2%	T1%	T2%	TT%	P%	PF%
B1	3.22	2.04	0.00	0.00	3.41	11.70	97.70
B2	15.25	7.70	0.00	3.70	0.00	0.00	95.00
F	0.00	0.00	0.00	0.00	0.00	2.10	99.00
L1	0.00	0.00	0.00	0.00	0.00	0.00	99.00
L2	4.90	0.00	0.00	0.00	0.00	0.56	98.80
L3	7.70	0.00	0.00	0.00	0.00	1.10	98.50
L4	20.00	0.00	0.00	0.00	11.00	0.00	78.60
L5	17.39	0.00	0.00	0.00	0.00	0.00	95.60
W1	0.00	11.00	0.00	0.00	0.00	1.50	98.60
W2	7.85	7.20	7.90	3.60	6.68	1.78	97.20
E1	0.00	0.00	0.00	0.00	2.80	0.00	97.90
E2	0.00	0.00	0.00	0.00	0.00	0.00	99.90

Abbreviations: n, A1, Anaphase-I cells with laggard chromosomes; A2, Anaphase-II cells with laggard chromosomes; T1, Telophase-I cells with laggard chromosomes; T2, Telophase-II cells with laggard chromosomes; TT, Tetrads with micronuclei; P, Pollen grains with extra-chromosome; PF, Pollen fertility.

Meiotic Abnormalities

The meiotic irregularities observed in *Avena* species and populations studied include: the occurrence of laggard chromosomes in anaphase I and II, telophase I and II, formation of micronuclei in tetrad cells, chromosomes stickiness, multipolar cell formation and cytomixis (Fig. 2, a-r), which have been discussed bellow.

Anaphase and Telophase Laggard Chromosomes

Data with regard to laggard chromosomes are provided in Table 2. Tehran population of *A. wiestii* showed formation of laggard chromosome from anaphase-I to telophase-II, while Dasht population of *A. eriantha*, Varamin population of *A. sterilis* ssp. *ludoviciana* and Esfahan population of *A. fatua* did not form any laggard chromosomes. These species also possessed the highest value of pollen fertility (Table 2).

The highest percentage of anaphase-I cells showing laggard chromosomes occurred in Mahalat and Dasht populations of *A. sterilis* ssp. *ludoviciana* (20.00 and 17.39 respectively), while the highest percentage of anaphase-II cells with laggard chromosomes occurred in Gonabad populations of *A. wiestii* (11.00).

Telophase-I laggard chromosomes were observed only in Tehran population of *A. wiesti* while the highest percentage of telophase-II cells showing laggard chromosomes occurred in Shiraz populations of *A. barbata* and Tehran population of *A. wiesti* (3.70 and 3.60 respectively).

Correlation test showed a negative significant correlation between pollen fertility and percentage of anaphase-I cells showing laggard chromosome and number of rod bivalents/ haploid chromosome number but showed a positive significant correlation with number of ring bivalents/ haploid chromosome number. However correlation test did not show any correlation between reduction in pollen fertility and the other meiotic abnormalities such as anaphase and telophase laggard chromosomes.

It has been suggested that infertility in polyploids is not solely due to the production of aneuploid gametes formed by improper segregation of chromosomes during anaphase/telophase stages, the genetic factors may also bring about pollen sterility as evidenced in different tetraploid strains of rye [10] as well as *Avena sativa* cultivars [1]. Therefore reduction in pollen fertility in *Avena* species studied may be also affected by genetic factors and not only by meiotic irregularities reported.

The correlation test showed a positive significant correlation between percentage of anaphase-II cells showing laggard chromosome and telophase-II cells showing laggard chromosome and also between telophase-I cells with laggard chromosome and telophase-II cells with laggard chromosome. Therefore micronuclei observed in tetrad cells may be formed due to laggard chromosomes occurring from anaphase-I onwards, although the role of cytomixis and chromosome migration among different meiocytes can not be ruled out (discussed bellow).

Chromosome Stickiness

Sticky chromosomes were observed from early stages of prophase and continued to the final stages of meiosis in most of the species studied (Fig. 2, j). Chromosome bridges resulting from stickiness were observed in anaphase-I and II as well as telophase-I and II stages (Fig. 2, k). The thickness of bridges observed and the number of chromosomes involved in their formation varied among different meiocytes and the species studied. Such a phenomenon has also been reported in Brazilian *Avena sativa* cultivars [1].

Genetic as well as environmental factors have been considered as the reason for chromosome stickiness in different plant species [17]. However Baptista-Giacomelli *et al*. [1], due to difference in the percentage of cells showing stickiness in different Brazilian *Avena sativa* cultivars suggested a genomic-environmental interaction as the main reason for the occurrence of chromosome stickiness which may holds true for the *Avena* species studied.

Multipolar Cells

An interesting observation was the occurrence of multipolar telophase-I cells in Shiraz population of *A. barbata* (Fig. 2, i). A similar phenomenon has been also reported in Brazilian *Avena sativa* cultivars [1] and in synthetic amphiploids of *Avena* [28].

The spindle apparatus is normally bipolar and acts as a single unit, playing a crucial role in alignment of metaphase chromosomes and their pole-ward movement during anaphase. Any distortion or break in spindle causes random sub-grouping of metaphase chromosomes which act independently [17]. Such abnormality may lead to the formation of aneuploid cells and chromosome mosaics as observed in some grass species including *Aegilops*×*Triticum* hybrids, amphidiploids of Triticineae and synthetic amphiploids of *Avena*, which is considered to be under control of the genes [28].

Cytomixis

Chromatin/chromosome migration occurred in different directions from early prophase to telophase-II in populations of *A. sterilis* ssp. *ludoviciana*, *A. eriantha*, *A. wiestii* and *A. barbata* (Fig. 2, m). Several metaphase/diakinesis cells in these species possessed extra or missing chromosomes showing aneuploid condition (Fig. 2, n). Such aneuploid cells would form aneuploid gametes. In fact several pollen grains possessed extra chromosomes in these populations.

A particular kind of cytomixis was observed in *A. eriantha*, *A. barbata*, *A. wiestii* and *A. ludoviciana*, leading to the migration of the whole chromosome complement. Such a whole chromosomes migration occurred in prophase-I and metaphase-I stages (Fig. 2, n & o), which may lead to the production of unreduced (2n) meiocytes as well as meiocytes with higher ploidy level. If such meiocytes form unreduced gametes, plants

with higher ploidy level would be formed. In fact plants with double chromosome number were observed in a single population of *A. eriantha* as discussed before. Formation of 2n gametes has been also reported in *A. vaviloviana* [13] and Brazilian cultivars of *A. sativa* [1].

Migration of chromatin material among the adjacent meiocytes occurs through cytoplasmic connections originated from the pre-existing system of plasmodesmata formed within the tissues of the anther. The plasmodesmata become completely obstructed by the deposition of callose, but in some cases they still persist during meiosis and increase in size forming conspicuous inter-meiocytic connections or cytomictic channels that permit the transfer of chromosomes [9]. Chromosome migration may also occur through cell wall dissolution among the neighboring meiocytes and forming syncyte [23].

Cytomixis is considered to be of less evolutionary importance but it may lead to production of aneuploid plants with certain morphological characteristics [22] or produce unreduced gametes as reported in several grass species including *Dactylis* [9] and *Aegilops* [24]. Unreduced gamete formation is of evolutionary importance leading to the production of plants with higher ploidy level.

Chromosome Elimination

Elimination of the micronuclei was noticed in a large number of telophase-I, and II cells as well as microspores released at the end of telophase-II of *A. eriantha* and *A. wiestii* in a different way from cytomixis, *i.e.* the micronuclei moved to the periphery of the cell from where, along with a small portion of the cell cytoplasm, were excluded (Fig. 2, q & r). A similar phenomenon has been reported in Brazilian cultivars of *A. sativa* [2] and Aegilops [24]. Chromosome elimination has been reported in other taxa too [17].

Different reasons have been suggested for chromosome elimination including: 1- slower growth rate of parental plant in the hybrids, 2- incorporation of a single chromosome into tiny vacuole-lysosome and fragmentation of interphase nuclei, 3- failure of chromosome alignment on metaphase, *etc.* [17].

B-chromosome

B-chromosomes (0-1) was observed in the *Avena* species and populations studied (Fig. 2, s-v). These chromosomes were smaller than the A-chromosomes and did not form any association with them. They could arrange themselves along with the A-chromosomes on the equatorial plane and move to the poles during anaphase.

B-chromosomes (Bs) are accessory chromosomes reported in more than 1300 species of Plants including *Avena* species [7] and almost 500 species of animals [5]. The B-chromosomes show numerical polymorphism and when present in high number affect negatively the growth and vigor of the plants, while in low number may benefit the plant possessing them. The Bs may affect the frequency and distribution of chiasma as well as chromosome association either directly or by affecting the genes controlling meiosis present on the A-chromosomes [26]. Some effects of B-chromosomes appear to be attributable directly to products of their genes as is the case in *A. sativa* in which the B-chromosomes' genes control resistance to rust [7].

Due to low number of meiocytes showing presence of B-chromosomes in *Avena* species studied, their effects on chiasma frequency and chromosome associations could not be worked out and need further studies.

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