MEIOTIC STUDIES OF SOME *AEGILOPS* (*POACEAE*) SPECIES AND POPULATIONS IN IRAN

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Thirteen populations of three *Aegilops* (*Poaceae*) species were analysed for meiotic characters including chiasma frequency and distribution, as well as chromosomal association and segregation. Populations of *A. triuncialis* and *A. cylindrica* possessed n = 14 chromosome number (tetraploid) while populations of *A. umbellulata* possessed n = 7 (diploid). Tetraploid species showed diplontic behavior and formed bivalents only. Cluster analysis of meiotic data showed distinctness of the species, although variations were observed in the chiasma frequency and distribution among different populations of each species. Cytomixis and chromosome elimination led to aneuploid and unreduced pollen mother cell formation in the species studied.

Keywords. Cluster analysis, cytomixis, meiotic analysis.

INTRODUCTION

The genus *Aegilops* (*Poaceae*) consists of more than 20 species distributed in SW and Central Asia and throughout the Mediterranean basin. A primary centre of diversity of the genus *Aegilops* is considered to be the Fertile Crescent, because a larger number of *Aegilops* species are found there than other areas (Slageren, 1994). Eig (1929) reported seven *Aegilops* species from Iran while Parsa (1950) reported ten species and Slageren (1994) twelve.

Aegilops species are considered as an important source of resistant genes for wheat and *A. squarrosa* L. as donor of the wheat D genome (Fan *et al.*, 1993; Bai *et al.*, 1995). Hence, extensive cytogenetical and hybridization studies have been performed on *Aegilops* species/populations in various parts of the world, considering polyploidy level, meiotic behavior and karyotypic details (Coucoli *et al.*, 1975; An *et al.*, 1985; Cunado, 1992). Although *Aegilops* species grow wild in various regions of Iran and are considered as important range grasses, there has been no cytogenetical report on them. The present paper provides basic cytogenetical information on 13 populations of three *Aegilops* species in Iran for the first time. An attempt is made to use cytogenetical data to elucidate the species inter-relationships.

MATERIALS AND METHODS

Plant material

Meiotic studies were performed on 13 populations of three *Aegilops* species, namely *A. triuncialis* L., *A. cylindrica* Host and *A. umbellulata* Zhuk. (Table 1). Voucher specimens are deposited in the herbarium of the Shahid Beheshti University (HSB).

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TABLE 1. *Aegilops* species and their localities.

Species	Locality	Species code	Voucher no.
Section *Aegilops*			
Aegilops triuncialis	Kerman	TR1	98276
A. triuncialis	Ivanegharb	TR2	98277
A. triuncialis	Gahvareh	TR3	98278
A. triuncialis	Noorabad	TR4	98279
A. triuncialis	Jazireh Islami	TR5	98280
A. umbellulata	Krandegharb	U1	98281
A. umbellulata	Ardekan	U2	98282
A. umbellulata	Ivanegharb	U3	98283
A. umbellulata	Sardasht	U4	98284
Section *Cylindropyrom*			
A. cylindrica	Gahvareh	CY1	98285
A. cylindrica	Sardasht	CY2	98286
A. cylindrica	Kerman	CY3	98287
A. cylindrica	Shahrekord	CY4	98288

Cytological preparation and meiotic analysis

The species/populations studied were grown under similar conditions in the experimental field of Iran National Genebank. Inflorescences having young flower buds were collected from 10 randomly selected plants from each species/populations and fixed in glacial acetic acid: ethanol (1:3) for 24h. Flower buds were washed and preserved in 70% ethanol at 4°C until used (Sheidai *et al.*, 1996).

Cytological preparations used squash technique and 2% aceto-orcein as the stain. Photomicrographs were taken at × 1000 magnification. One hundred pollen mother cells (PMCs) were analysed for chiasma frequency and distribution at diakinesis/metaphase stage and 1000 PMCs were analysed for chromosome segregation during the anaphase and telophase stages. Pollen fertility was checked by staining a minimum of 1000 pollen grains from each taxon using acetocarmine: 50% glycerin (1:1) for 1h. Well-stained and perfect pollen grains were taken as fertile, while unstained/empty pollens were considered as infertile (Sheidai & Inamdar, 1992).

In order to group the species/populations having similar meiotic behaviour, single linkage and Ward's minimum variance clustering methods were used (Romesburg, 1984; Sheidai *et al.*, 1998). For cluster analyses variables (characters) were standardized (mean = 0, variance = 1: Chatfield & Collins, 1995).

In order to determine the most variable meiotic characters, principal components analysis (PCA) was performed on standardized meiotic data from different populations of each species separately. Ordination of the taxa was performed on the first two PCA axes (Sheidai & Alishah, 1998). Multivariate statistical analyses used STATISTICA ver.4.3 (1993) software.

RESULTS AND DISCUSSION

Chiasma frequency, chiasma distribution and chromosome association

Data with regard to chiasma frequency and distribution, as well as chromosomal association, is presented in Table 2 (Fig. 1: 1–25). The populations of *A. triuncialis* studied possessed n = 14 (4x) chromosome number (Fig. 1: 4–6) supporting the previous report (An *et al.*, 1985). The Ivanegharb population showed the highest values for total, terminal and intercalary chiasma as well as ring bivalents (28.10, 24.57 3.53 and 12.60 respectively). The Noorabad population possessed the least values for chiasma as well as ring bivalents (23.50, 21.94 and 1.56 respectively).

Some of the metaphase cells showed clumping and stickiness of the chromosomes while some of the anaphase-I and II as well as telophase-I and II cells showed presence of 1–4 laggard chromosomes (Fig. 1: 10). Such laggard chromosomes would lead to micronuclei formation at the end of telophase-I and II, which remained in most of the cells even till the formation of pollen grains. Such anomalies might be the reason for low pollen fertility of these populations (Table 3).

Single linkage and Ward's cluster analyses of *A. triuncialis* populations based on meiotic data produced the same results (Fig. 2). The Gahvareh and Jazireh Islami populations are joined at 2-linkage distance showing more similarity than the other populations, while the Noorabad population stands in a separate cluster far from the other two because of a difference in meiotic characters. Ordination of these populations on the first two principal components supported the clustering results.

Principal components analyses (PCA) of the meiotic data revealed that the first two components comprise about 99% of the total variance in which intercalary chiasma, ring and rod bivalents possessed the highest correlation (>0.90). These are the most variable meiotic characters among the *A. triuncialis* populations studied.

Populations of *A. cylindrica* studied possessed n = 14 (4x) chromosome number, (Fig. 1: 7–9), supporting the previous report (An *et al.*, 1985). The Sardasht and Kerman populations showed the highest value of total (30.75 and 30.60 respectively) and intercalary chiasma (7.25 and 8.80 respectively), while the Gahvareh population possessed the highest value of rod bivalents showing a low pollen fertility (93%). Univalents were only formed in this population (Table 2).

Clumping and stickiness of chromosomes were observed in some of the metaphase cells while laggard chromosomes (1–4) and micronuclei were formed in anaphase and telophase cells (Fig. 1: 11).

Gahvareh and Kerman populations showed the highest percentage of anaphase and telophase cells possessing laggard chromosomes as well as tetrads and pollen grains possessing extra-chromatin material. These populations showed low pollen fertility (Table 3). The Sardasht population possessed a low value for the cells with laggards and extra-chromatin materials but a high value of cytomictic cells (will be discussed in the following paragraphs), which might be the reason for its low pollen fertility.

The phenogram obtained from cluster analyses of *A. cylindrica* populations based

TABLE 2. Meiotic details of Iranian *Aegilops*. Species code as Table 1. Abbreviations: TX, terminal chiasma; IX, intercalary chiasma; TO, total chiasma; R, ring bivalent; RD, rod bivalent; I, univalent; TXB; total chiasma/bivalent; IXB, intercalary chiasma/bivalent; TOB, total chiasma/bivalent; RC, ring bivalent/gametic chromosome number; RDC, rod bivalent/gametic chromosome number; IC, univalent/gametic chromosome number, n, gametic chromosome number; x, ploidy level.

Species	TX	IX	TO	R	RD	I	TXB	IXB	TOB	RC	RDC	IC	n	x
TR1	23.68	3.37	27.06	11.43	2.56	0.00	1.69	0.24	1.93	0.82	0.18	0.00	14	4x
TR2	24.57	3.53	28.10	12.60	1.39	0.00	1.76	0.25	2.01	0.90	0.10	0.00	14	4x
TR3	23.57	2.19	25.76	10.83	3.16	0.00	1.68	0.16	1.84	0.77	0.23	0.00	14	4x
TR4	21.93	1.56	23.50	9.50	4.50	0.00	1.57	0.11	1.68	0.68	0.32	0.00	14	4x
TR5	22.62	3.06	25.68	10.50	3.50	0.00	1.62	0.22	1.83	0.75	0.25	0.00	14	4x
U1	11.58	1.46	13.14	6.00	1.00	0.00	1.65	0.21	1.88	0.86	0.14	0.00	14	4x
U2	11.73	1.31	13.05	5.89	1.07	0.00	1.68	0.19	1.86	0.84	0.15	0.00	14	4x
U3	11.96	2.80	14.76	6.44	0.56	0.00	1.71	0.40	2.11	0.92	0.08	0.00	14	4x
U4	10.50	4.38	14.88	5.88	1.00	0.16	1.50	0.63	2.13	0.84	0.14	0.02	14	4x
CY1	23.55	2.48	26.03	11.44	2.41	0.41	1.68	0.18	1.86	0.82	0.17	0.03	7	2x
CY2	23.50	7.25	30.75	12.56	1.46	0.00	1.68	0.52	2.20	0.90	0.10	0.00	7	2x
CY3	21.81	8.80	30.60	13.10	0.88	0.00	1.56	0.63	2.19	0.94	0.06	0.00	7	2x
CY4	21.48	6.51	28.00	12.51	1.28	0.00	1.53	0.47	2.00	0.89	0.09	0.00	7	2x

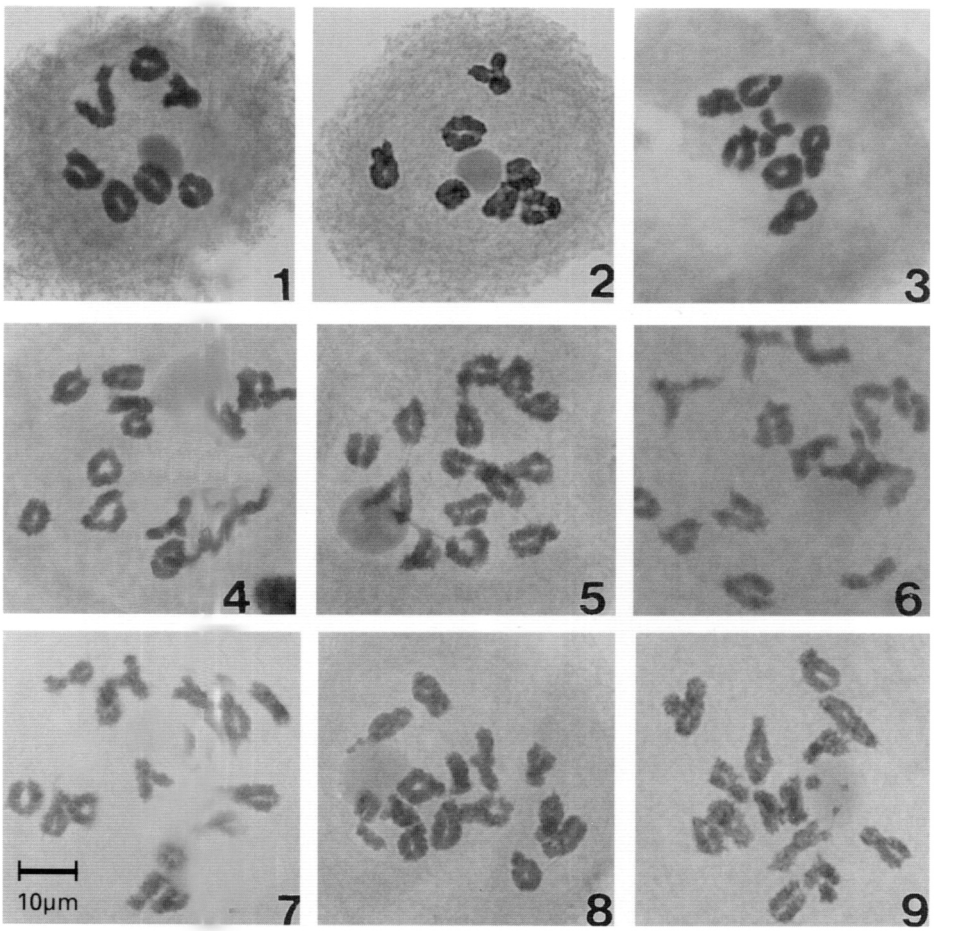
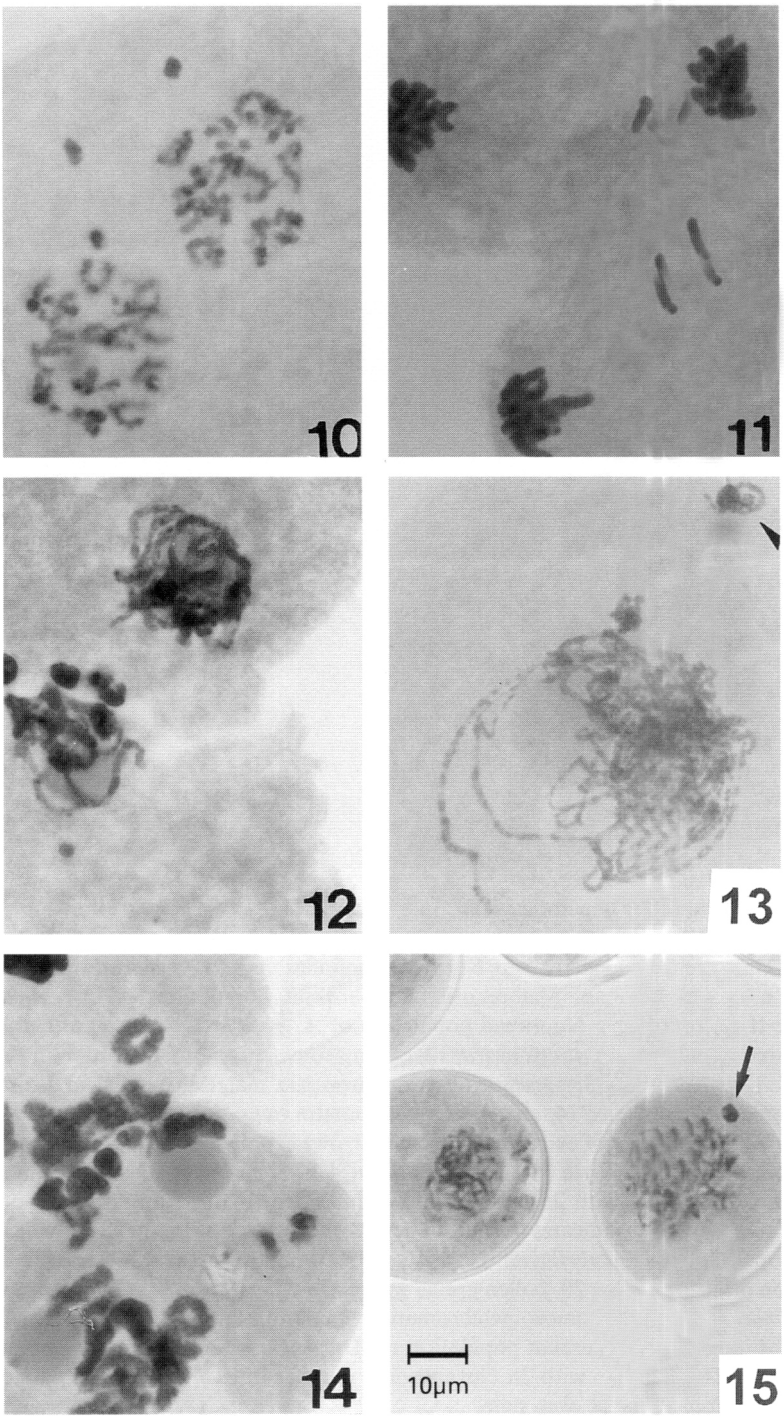


FIG. 1. Representative meiotic cells in *Aegilops* 1–3, meiocytes showing n = 7 in Karandegharb, Fars and Ivanegharb populations of *A. umbellulata*; 4–6, meiocytes showing n = 14 in Gahvareh, Ivanegharb and Noorabad populations of *A. triuncialis*; 7–9, meiocytes showing n = 14 in Kerman, Shahrekord and Sardasht populations of *A. cylindrica*; 10, telophase-II micronuclei in Noorabad population of *A. triuncialis*; 11, laggard chromosomes in Gahvareh population of *A. cylindrica*; 12, chromosome/chromatin migration in Fars population of *A. umbellulata*; 13, presence of extra-chromatin material (arrow) in Jazireh Islami population of *A. triuncialis*; 14, chromosome/chromatin migration in Sardasht population of *A. cylindrica*; 15, presence of extra-chromosome (arrow) in pollen grain in Sardasht population of *A. cylindrica*; 16, meiocyte showing the loss of 4 bivalents in Sardasht population of *A. cylindrica*; 17, meiocyte with 2n chromosome number (n = 14) in Karandegharb population of *A. umbellulata* (arrow indicates the nucleolus); 18, meiocyte showing 1 extra-bivalent (arrow) in Fars population of *A. umbellulata*; 19, meiocyte showing the loss of 4 bivalents in Gahvareh population of *A. cylindrica*; 20, pollen grains with extra-chromosome in Gahvareh population of *A. cylindrica*; 21–23, chromosome/chromatin elimination (arrow) in Karandegharb population of *A. umbellulata*, Kerman population of *A. triuncialis* and Shahrekord population of *A. cylindrica*; 24, meiocyte with 2n chromosome number in *A. cylindrica*; 25, anaphase cell showing 28 chromosome at each pole.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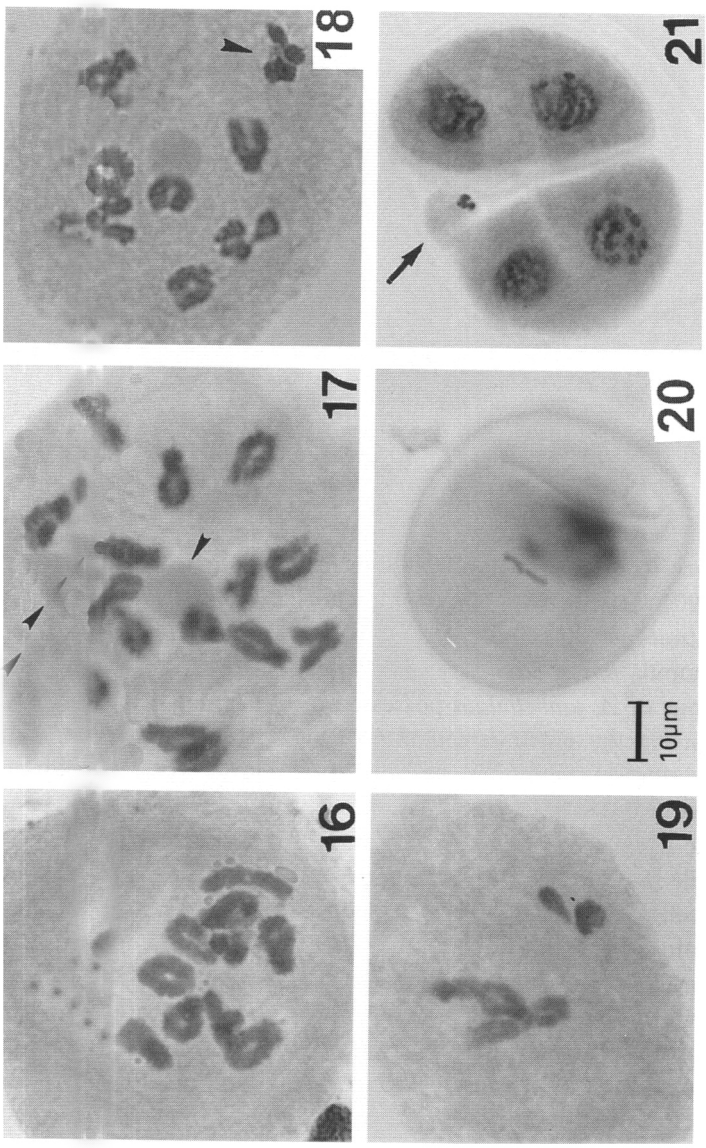
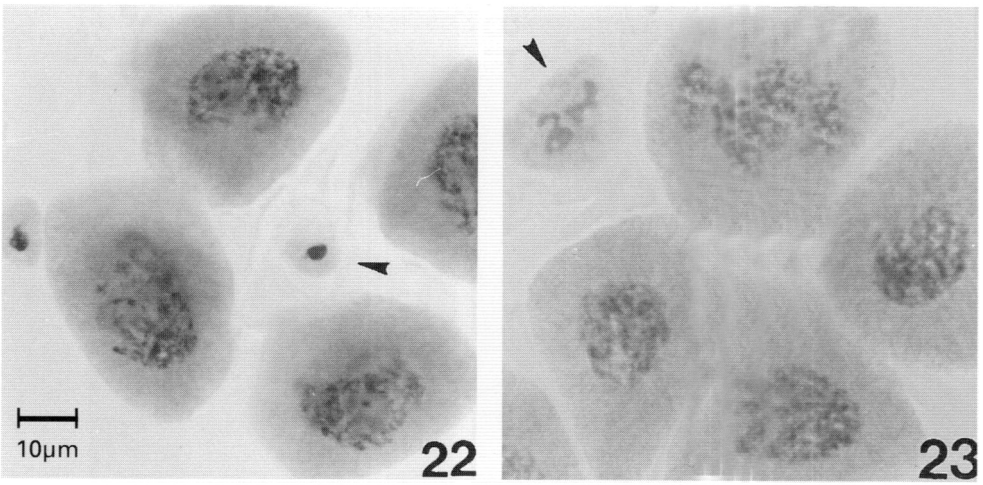


on meiotic data is presented in Fig. 3. Two major clusters are formed. The first cluster is comprised of the Shahrekord, Kerman and Sardasht populations while the Gahvareh population formed the second cluster because of differences in its meiotic characters. Ordination of *A. cylindrica* populations on the first two principal components supported the clustering results.

Principal components analyses of meiotic data performed among populations of *A. cylindrica* revealed that the first two PCA components comprise about 98% of



total variance. Total chiasma and ring bivalents possessed the highest positive correlation (>0.90) with the first component, while univalents possessed the highest negative correlation (−0.90). These are the most variable meiotic characters among *A. cylindrica* populations.

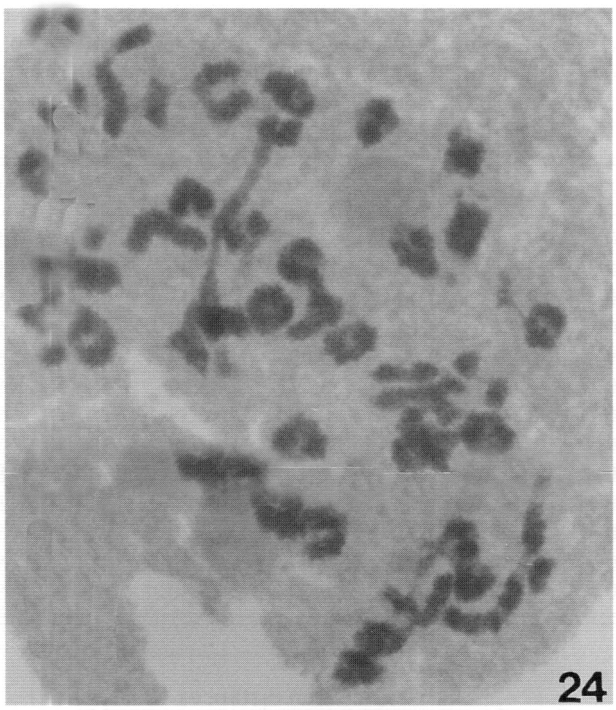
Populations of *A. umbellulata* possessed n=7 (2x) chromosome number (Fig. 1: 1–3) supporting the previous report (An *et al.*, 1985). Sardasht and Ivanegharb populations showed the highest value of total and intercalary chiasma. Univalents were formed in the Sardasht population only.

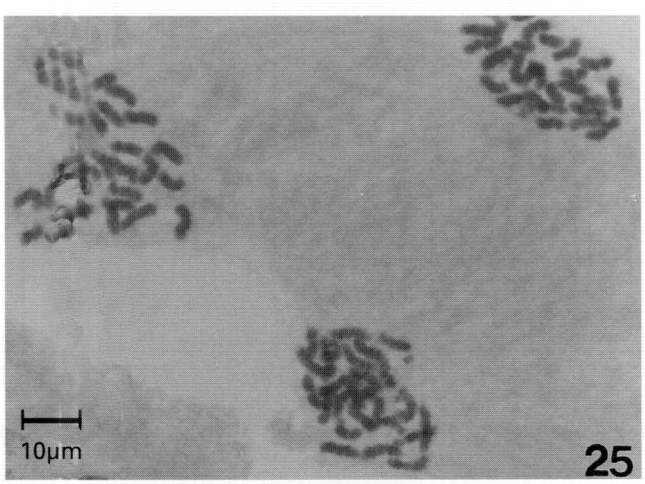
Anaphase-I laggards (1–2) were formed in the Sardasht and Ivanegharb populations, while the Sardasht population possessed micronuclei and highest value for cytomictic cells. This population possessed lower pollen fertility (96%) than the other two populations.

The phenogram obtained from cluster analyses of *A. umbellulata* populations based on meiotic data is presented in Fig. 4. The Fars and Karandegharb populations showed more similarity and formed the first cluster, while the Ivanegharb and Sardasht populations, because of differences in their meiotic characters, formed a separate cluster. Ordination of these populations on the first two principal components supported the clustering results.

Principal components analyses of meiotic data performed among populations of *A. umbellulata* revealed that the first two PCA components comprise about 99% of total variance. In the first component intercalary chiasma and univalents and in the second component ring bivalents possessed high correlation (>0.90), hence these are the most variable meiotic characters among the *A. umbellulata* populations studied.

Variation in chiasma frequency and localization is genetically controlled (Rees & Jones, 1977; Quicke, 1993) and has been reported in *A. speltoides*, *Lolium* and *Festuca* populations too (Coucoli *et al.*, 1975; Rees & Jones, 1977). 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 (Rees & Dale, 1974).

Differences observed in chiasma frequency and distribution in *Aegilops* species/populations studied reflect partly their genomic differences as these plants were grown

TABLE 3. Cells having laggard chromosomes and micronuclei (species code as Table 1). Abbreviations: 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, C, cytomictic cell.

Species	A1%	A2%	T1%	T2%	TT%	P%	PF%	C%
TR1	3.00	19.40	0.00	2.63	5.17	6.30	89.60	3.50
TR2	11.10	27.60	0.00	3.84	2.90	0.40	94.20	2.50
TR3	8.90	8.40	0.00	2.10	3.38	0.30	93.60	6.57
TR4	5.40	1.37	8.10	0.00	7.30	1.12	92.00	12.70
TR5	2.19	0.00	0.00	0.00	1.00	1.00	95.00	20.80
CY1	10.00	4.30	6.80	3.57	3.80	5.79	94.00	3.80
CY2	2.10	2.50	0.00	0.00	6.38	1.78	90.60	6.38
CY3	7.50	0.00	5.40	0.00	1.38	3.50	95.60	1.38
CY4	6.70	2.30	1.48	0.00	2.62	1.30	97.00	2.62
U1	0.00	0.00	0.00	0.00	3.80	0.00	97.20	3.80
U2	0.00	0.00	0.00	0.00	3.20	0.00	99.10	3.20
U3	6.30	0.00	0.00	0.00	5.10	0.00	96.90	5.10
U4	3.30	0.00	1.60	0.00	16.40	0.00	96.20	16.40

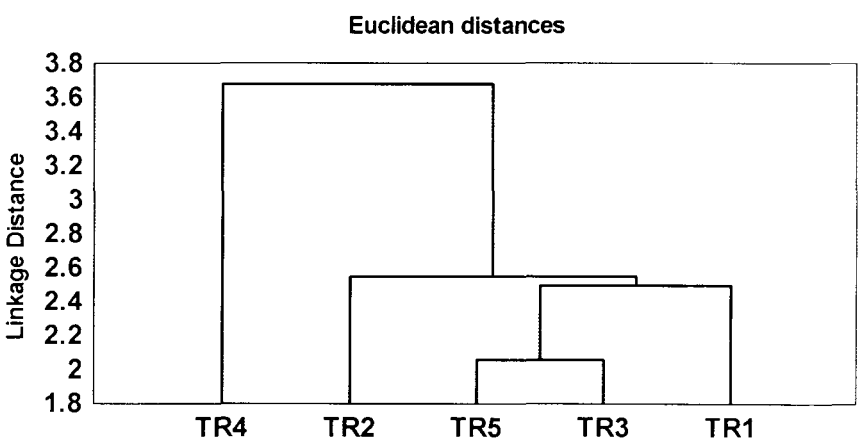


FIG. 2. Single linkage cluster analysis of meiotic data in *A. triuncialis*, species code as Table 1.

under uniform conditions in the experimental field. Such genomic variations, if combined with the other characteristics, can be used for genetic and breeding purposes.

A. triuncialis and *A. cylindrica* are tetraploid (2n = 4x = 28) and are expected to form one to few quadrivalents in metaphase/diakinesis stages, although they formed only bivalents showing diplontic behavior (Table 1). Such a diplontic behavior might result from the small size of chromosomes, restricting the chiasma formation among bivalents only, or because of genomic control as in hexaploid wheat (Clark & Wall,

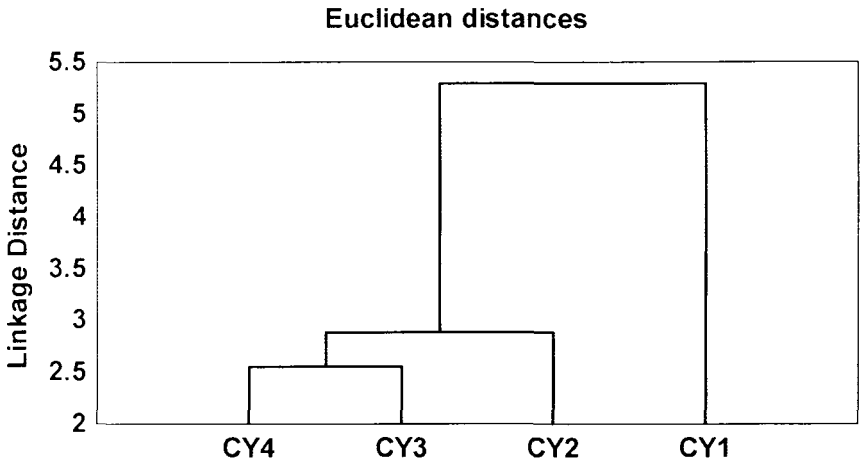


FIG. 3. Single linkage cluster analysis of meiotic data in *A. cylindrica*, species code as Table 1.

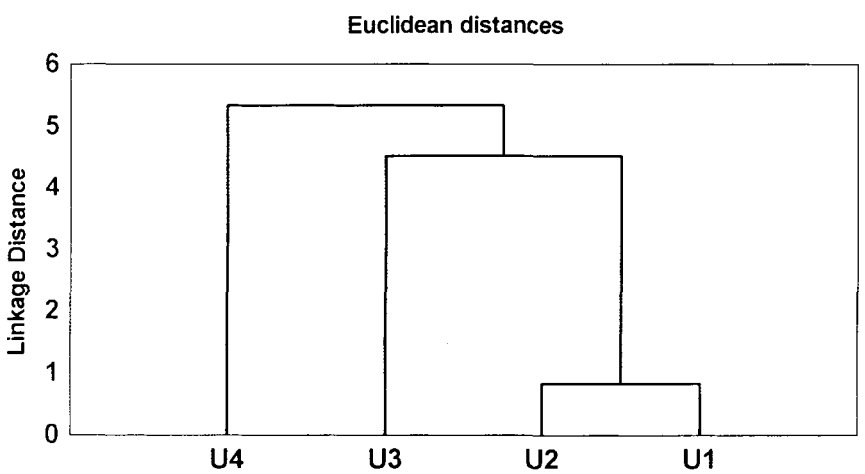


FIG. 4. Single linkage cluster analysis of meiotic data in *A. umbellulata*, species code as Table 1.

1996). The size of chromosomes in the species studied ranged from 8–15μm (unpublished data), which is quite large, hence the size of chromosomes is not a limiting factor and a genomic control might operate in *A. triuncialis* and *A. cylindrica*. Chromosome segregation during anaphase occurs normally from bivalent leading to high pollen fertility.

Cunado (1992) studied chromosomal association in some diploid and polyploid *Aegilops* species, reporting diplontic behavior in some of the polyploid species, while the others formed quadrivalents. It was argued that the genomic control operating in some of the polyploid *Aegilops* species caused the bivalent formation.

The phenogram obtained from cluster analyses of the *Aegilops* species/populations

studied based on meiotic data (Table 1), is presented in Fig. 5. Three major clusters are formed at 3.5-linkage distance corresponding to the three different species studied. Populations of the *A. triuncialis* comprise the first cluster, populations of *A. cylindrica* comprise the second cluster and different populations of *A. umbellulata* form the third cluster. Separation of these different species and their populations in three separate groups indicates distinctness of the species in their meiotic behaviour.

In the cluster analysis of the meiotic data (Fig. 5), populations of *A. umbellulata* show more similarity to the populations of *A. cylindrica* which is not consistent with their taxonomic positions and genomic constituents (Slageren, 1994). *A. triuncialis* and *A. umbellulata* belong to section *Aegilops* and are considered as U genome species while *A. cylindrica* belongs to section *Cylindropyrom* and is a D genome species (Okuno *et al.*, 1998).

The meiotic characters used for cluster analyses (Fig. 5) are under the influence of polyploidy level. *Aegilops triuncialis* and *A. cylindrica* are tetraploid (2n = 4x = 28), while *A. umbellulata* is diploid (2n = 2x = 14). To avoid the effect of ploidy level, chiasma frequency and distribution/bivalent was used for clustering and ordination (Fig. 6).

When the Gahvareh population of *A. cylindrica* (CY1) and the Sardasht population of *A. umbellulata* (U4) (which showed much differences in their meiotic characters compared with the other populations) were omitted from the analyses, a better grouping was obtained; hence U genome species of *A. triuncialis* and *A. umbellulata* were grouped together (Fig. 6) supporting their taxonomic treatment.

SDS–seed protein analyses of these species (unpublished data) produced the same results, indicating distinctness of the species as well as inter-relationship among D genome and among U genome *Aegilops* species. Molecular studies using RAPD markers performed on the U and D genome *Aegilops* species collected from Central

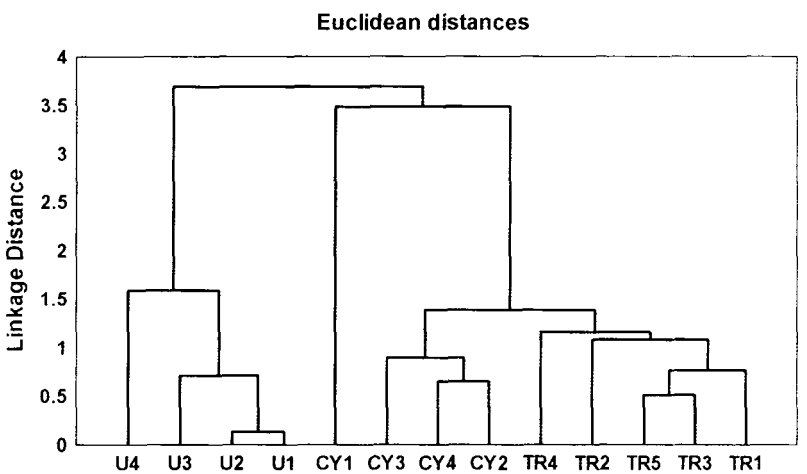


FIG. 5. Single linkage cluster analysis of meiotic data in *Aegilops* taxa, species code as Table 1.

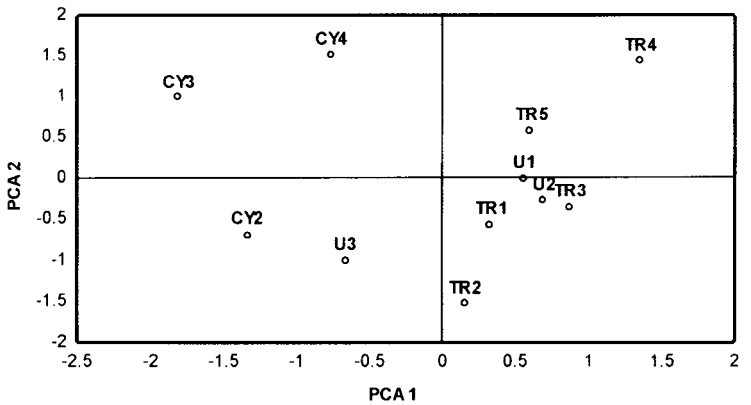


FIG. 6. Ordination of the meiotic data, species code as Table 1.

Asia (Okuno *et al.*, 1998) also showed similarity of the genetic structure among D genome and among the U genome species. Therefore, meiotic data along with other characteristics such as seed proteins might have taxonomic value.

Cytomixis

Chromatin/chromosome migration occurred in different directions from early prophase to telophase-II (Fig. 1: 12–14).

Several metaphase/diakinesis cells in the Sardasht and Gahvareh populations of *A. cylindrica*, as well as the Fars and Karandegharb populations of *A. umbellulata*, possessed extra-chromosomes showing aneuploid condition (Fig. 1: 18). Such aneuploid cells would form aneuploid gametes, in fact several pollen grains having extra-chromosomes were obtained in these populations (Fig. 1: 15, 20). Metaphase/diakinesis cells with reduced chromosome number were also observed (Fig. 1: 16, 19). Both of these aneuploid conditions might reduce the fertility of plants. A particular kind of cytomixis was observed in these two populations leading to the migration of whole chromosome complement and production of unreduced (2n) gametes. About ⅓ of the metaphase/diakinesis cells in the Karandegharb population of *A. umbellulata* possessed n = 14, double the normal gametic number i.e. n = 7 (Fig. 1: 17). Such cells might be formed as a result of either anaphase non-disjunction or syncyte formation through cytomixis. Because no complete anaphase non-disjunction was observed, cytomixis might be the reason for 2n cells produced.

In the Gahvareh population of *A. cylindrica* several flower buds possessed meiocytes with 2n = 28 chromosome number (Fig. 1: 24). Such cells were bigger in size compared to the n = 14 pollen mother cells (PMCs). Anaphase segregation of chromosomes also revealed the presence of 28 chromosomes in each pole (Fig. 1: 25), supporting the presence of 2n PMCs. If such meiocytes form unreduced pollen grains (to be investigated after larger sampling of pollen grains), plants with higher poly-

ploidy level could be obtained. A similar type of cytomixis has been reported in *Dactylis glomerata* subsp. *castellata* (Falistocco *et al.*, 1995).

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 (Heslop-Harisson, 1966), 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 (Risueño *et al.*, 1968; Falistocco *et al.*, 1995). Occurrence of cytomixis and chromatin migration has also been reported in *A. ovata* × *Triticum monococcum* (Percival, 1930).

Chromosome elimination

Elimination of the micronuclei was noticed in a large number of telophase-II cells of *A. triuncialis*, *A. cylindrica* and *A. umbellulata* 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. As a result, several micro-cells possessing one or few chromatin materials were formed (Fig. 1: 21–23). Chromosome elimination has been reported in other taxa too (Nirmala & Panuganti, 1996).

In short the present study indicates distinctness of meiotic behavior in the *Aegilops* species studied and reports cytomixis and chromosome elimination in these species for the first time.

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