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Cytology of some Iranian *Stipa* (Poaceae) species and populations

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Meiotic studies were performed on 16 populations of 13 *Stipa* species concerning polyploidy level, chiasma frequency and distribution, chromosome association and segregation. The species and populations studied possessed 2n = 24, 36 and 44 chromosome number. The chromosome numbers of four species are reported for the first time. The populations and species studied differed significantly in their meiotic characteristics. Meiotic abnormalities observed included laggard chromosome formation, stickiness and cytomixis. Cytomixis led to the formation of aneuploid meiocytes. Unreduced pollen grains were observed in some of the species, which differed significantly in their size compared to the normal (reduced) pollen grains.

Key words: chiasma frequency, polyploidy level, *Stipa*.

Introduction

The genus *Stipa* (Poaceae) is composed of 300–400 species throughout the world with about 90–100 species distributed in the old world (FREITAG 1985, BARKWORTH and EVERETT 1987). The discrepancy in the number of *Stipa* species is due to the taxonomic problems existing in this genus (VAZQUEZ 1997).

The genus *Stipa* possesses both annual and perennial species, usually growing in arid and dry regions; however, some species with primitive, morphological characteristics grow in semi-arid regions too (FREITAG 1985).

Stipa species are among the important forage plants of Iran and are distributed in various regions of the country. The number of *Stipa* species growing in Iran varies from 6 to 18 according to different authors (PARSA 1950, BOR 1968). Although the available literature dealing with systematics, biosystematics and cytogenetics of *Stipa* species indicates the importance of these taxa (FREITAG 1985, TZVELEV 1977, 1989), no report is available on the cytogenetics of *Stipa* species and populations from Iran. Therefore the present study considers a meiotic analysis of 16 populations of 13 *Stipa* species in Iran, trying to reveal the ploidy level and the basic cytogenetic information of these species for the first time.

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Materials and methods

Meiotic studies were performed on 16 populations of 13 *Stipa* species belonging to 4 different sections (Tab. 1) namely: 1- Section *Lasiagrostis* (Link.) Hackel., including *St. caragana* and *St. haussknechtii*, 2- Section *Stipella* Tzvelev emend. Freitag., including *St. parviflora* and *St.capensis*, 3- Section *Stipa* L., including *St. lessingiana* Trin. et Rupr., *St. turkestanica* Hackel. and *St. pennata* L. from the species group 1 (Eriostipa) as well as *St. caucasica* Schmalh. From the species group 2 (Brevigeniculata), 4- Section *Barbatae* Junge emend. Freitag., including *St. arabica* Trin. et Rupr. (three populations), *St. hohenackeriana* Trin. et Rupr., *St. ehrenbergiana* Trin. et Rupr. and *St. iranica* Freitag. and *St. holosericea* Trin. (two populations, Tab. 1).Voucher specimens are deposited in the Herbarium of Shahid Beheshti University (HSBU).

For cytological studies young flower buds were collected from 10 randomly selected plants of each species/ population and fixed in glacial acetic acid: ethanol (1:3) for 24 hrs. Flower buds were washed and preserved in 70% ethanol at 4 °C until used (SHEIDAI et al. 1999). Cytological preparations used squash technique and 2% aceto-orcein as the stain.

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 a minimum 1000 pollen grains with 2% acetocarmine: 50% glycerin (1:1) for about ½ hour. Round/complete pollens which were stained were taken as fertile, while shrunken/incomplete pollens with no stain were considered as infertile (SHEIDAI et al. 1999).

In order to detect a significant difference in chiasma frequency and distribution as well as chromosomes association, analysis of variance (ANOVA) followed by the least significant difference test (LSD) was performed among tetraploid species (SHEIDAI et al. 2002).

In order to detect a significant difference in meiotic abnormalities, χ^2 test was performed among different species and populations. For grouping the species and populations showing similar meiotic behavior, different methods of single linkage, UPGMA and WARD clustering as well as ordination based on principal components analysis (PCA) was performed on standardized data (mean = 0, variance = 1, SHEIDAI et al. 2002). Univariate and multivariate statistical analyses used SPSS ver. 9 (1998) software.

Results and discussion

Chromosome number and ploidy level

We present data with regard to meiotic chromosome number, ploidy level, chiasma frequency and distribution, as well as chromosome pairing (Tab. 1, Fig. 1)**.** The species and populations studied possessed 2n = 24, 36 and 44 chromosome numbers. Considering x = 9, 11 and 12 as the basic chromosome numbers of the genus *Stipa* (FREITAG 1985, WATSON and DALLWITZ 1992), the species and populations studied are diploid and tetraploid (4x).

To our knowledge, the chromosome number of *Stipa hohenackeriana* (2n = 44), *St. ehrenbergiana* (2n = 44), *St. iranica* (2n = 44), *St. caragana* (2n = 24) and *St. haussknechtii* (2n = 44) are reported here for the first time.

Tab. 1. Meiotic characteristics studied in the *Stipa* species and populations. TX – Terminal chiasmata, IX = Intercalary chiasmata, TOX = Total chiasmata, RII – Ring bivalent, RDII = Rod bivalent, IV = Qudrivalent, I = Univalent, TXN -Terminal chiasmata/n, IXN – Intercalary chiasmata/n, TOXN – Total chiasmata/n.

No. Species	Locality	TX	IX	TOX	RII	RDII	IV	I	TXN	IXN	TOXN	2n
Sec. *Lasiagrostis* (Link.) Hackel.												
1 *St. caragana*	Firoozkooh	18.64	1.46	20.10	7.25	4.68	0.00	0.14	1.55	0.12	1.61	24
2 *St. haussknechtii*	Isfahan	34.47	1.10	35.60	13.50	8.00	0.17	0.20	1.57	0.05	1.62	44
Sec. *Stipella* Tzvelev emend. Freitag												
3 *St. parviflora*	Mahallat	28.66	3.46	32.12	7.76	13.39	0.44	0.05	1.30	0.16	1.37	44
4 *St. capensis*	Loshan	30.20	0.55	30.75	12.75	5.25	0.00	0.00	1.68	0.03	1.71	36
Sec. *Stipa* L.												
Species group 1												
5 *St. lessingiana*	Tehran	30.80	5.80	36.60	12.63	3.43	0.00	0.06	1.40	0.26	1.63	44
6 *St. turkestanica*	Tehran	34.48	5.48	39.96	14.64	1.76	0.00	0.00	1.56	0.24	1.81	44
7 *St. pennata*	Dasht	29.81	1.11	30.92	8.69	13.15	0.00	0.00	1.35	0.05	1.41	44
Species group 2												
8 *St. cacausica*	Dasht	27.19	6.03	33.22	9.30	6.19	0.00	0.76	1.23	0.27	1.51	44
Sec. *Barbatae* Jung emend. Freitag.												
9 *St. arabica*1	Meshkinshahr	36.82	1.97	38.79	15.26	4.41	0.02	0.52	1.67	0.08	1.76	44
10 *St. arabica*2	Tehran	36.44	2.60	39.04	15.84	3.16	0.04	0.60	1.65	0.11	1.77	44
11 *St. arabica*3	Meiyaneh	36.80	1.22	38.02	15.80	4.51	0.09	0.38	1.67	0.05	1.73	44
12 *St. hohenackeriana*	Meshkinshahr	38.59	1.59	40.18	17.85	2.25	0.00	0.37	1.75	0.07	1.82	44
13 *St. ehrenbergiana*	Meiyaneh	37.30	3.56	40.86	16.60	1.66	0.00	0.33	1.69	0.16	1.85	44
14 *St. iranica*	Tehran	32.88	4.66	37.44	14.14	2.85	0.03	0.51	1.49	0.20	1.70	44
15 *St. holosericea*	Damavand	31.86	5.73	37.66	12.46	3.23	0.03	0.80	1.44	0.26	1.71	44
16 *St. holosericea*	Meiyaneh	34.88	4.94	39.83	14.33	2.55	0.05	0.33	1.58	0.22	1.81	44

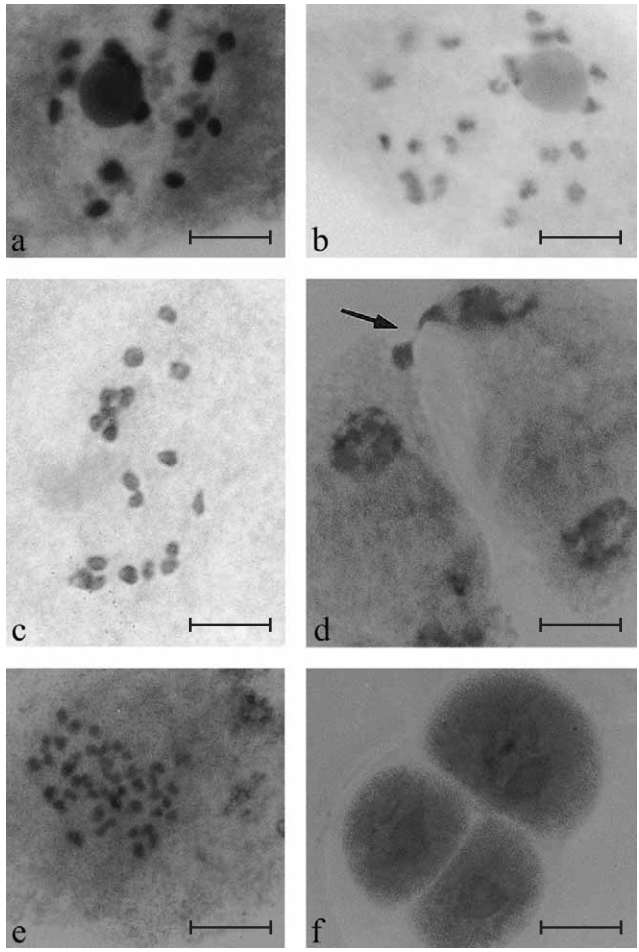

Fig. 1. Representative miotic cells in *Stipa* species studied. a – *Stipa capensis* (n = 18), b – *St. pennata* (n = 22), c – *St. haussknechtii* (n = 22), d – Cytomixis (arrow) in *St. ehrenbergiana*, e – Meiocyte showing aneuploidy in *St. holosericea*, f – A triad in telophase II of *St. ehrenbergiana* showing unreduced cell formation. Scale bar = 10 μm.

FREITAG (1985) reported 2n = 40 for *St. turkestanica* while the present study reports a new ploidy level i.e. n = 22 (2n = 4x = 44) for this species. Similarly, VÁZQUEZ and DEVESA (1996) reported 2n = 2x = 28 for *St. parviflora* while the present study reports a new ploidy level i.e. n = 22 (2n = 4x = 44) for this species.

The chromosome numbers reported in this study for *St. lessingiana*, *St. caucasica,* St. *arabica* and *St. holosericea* (2n = 44) support the earlier reports of MAGULAEV (1984) and STRID (1987), while the chromosome numbers reported for *St. capensis* (2n = 2x = 36) and *St. pennata* (2n = 4x = 44) support the earlier reports of VÁZQUEZ and DEVESA (1996) as well as KRANSNIKOV (1991) respectively. The occurrence of two different chromosome numbers of n = 20 (2n = 40) and n = 22 (2n = 44) in a single species i.e. *St. turkestanica* and 2n = 2x = 28 and 2n = 4x = 44 in *St. parviflora* is also reported for other *Stipa* species such

as *St. leucotricha* (2n = 26 and 28, LOVE 1974), *St. lemmonii* (2n = 34 and 36, STEBBINS and LOVE 1941) and *St. bromoides* (2n = 24 and 28, STRID and ANDERSON 1985, VÁZQUEZ and DEVESA 1996). Therefore we may suggest that along with hybridization and allopolyploidy (STEBBINS 1987), the occurrence of aneuploidy may have also played a role in the speciation of the genus *Stipa*. However, the mechanism(s) of aneupolidy production in the genus *Stipa* is not known.

Chromosomes pairing and chiasma frequency

Among the *Stipa* species and populations having 2n = 44 chromosome number the highest mean number of total and terminal chiasmata occurred in *St. ehrenbergiana* (40.86, Tab. 1), while the lowest values occurred in *St. caragana* (20.12). The highest value of intercalary chiasmata occurred in *St. lessingiana* (5.80) while the lowest value occurred in *St. haussknechtii* and *St. pennata* (1.10 and 1.11 respectively).

The highest value of ring bivalents occurred in *St. hohenackriana* (17.85) while the lowest value occurred in *St. caragana* (7.25). The highest value of rod bivalents occurred in *St. parviflora* (13.39), while the lowest value occurred in *St. ehrenbergiana* (1.66). The *Stipa* species have previously been considered as allopolyploid originated from inter-specific hybridization followed by chromosome doubling (TZVELEV 1977) and are expected to form merely bivalents. However some of the tetraploid species studied showed the presence of quadrivalents (Tab. 1), possibly due to the occurrence of chromosomal structural changes. Such a chromosomal repatterning after doubling of chromosome number is considered an important factor in the evolution of Graminea (STEBBINS 1987).

Among the species/ populations showing quadrivalent formation, the highest value of quadrivalents occurred in *St. parviflora* (0.44) and the lowest value occurred in the Meshkinshahr population of *St. arabica* (0.02). ANOVA and LSD tests performed on chiasma frequency and distribution as well as chromosomal association among *Stipa* species and populations having 2n = 44 revealed a significant difference in most of the meiotic characteristics among the species studied, indicating genomic differences.

Variation in chiasma frequency and localization is genetically controlled and is reported in populations of different grass species like *Aegilops* (COUCOLI et al. 1975), *Lolium* and *Festuca* as observed in the species/ populations of *Stipa*. Such a variation in the species/ populations with the same chromosome numbers is considered as a means for generating new forms of recombination influencing the variability within natural populations in an adaptive way (REES and DALE 1974).

Since our previous studies on cytogenetics of *Aegilops* species showed that meiotic characteristics can be used to illustrate the species inter-relationships supporting the taxonomic treatments of the genus (SHEIDAI et al. 1999, 2002), a similar analysis was performed in this work in order to investigate the species interrelationships among the *Stipa* species studied.

Different methods of cluster analysis and ordination based on cytogenetic characters were performed which produced almost similar results (Figs. 2 and 3). In both analyses 3 major clusters /groups are formed. The first major cluster comprises two sub-clusters; the species of *St. arabica*, *St. hohenackeriana* and *St. ehrenbergiana* of the sec. *Barbatae* are placed together in the first sub-cluster/ group supporting FRITAG (1985) taxonomic treatment of the genus.

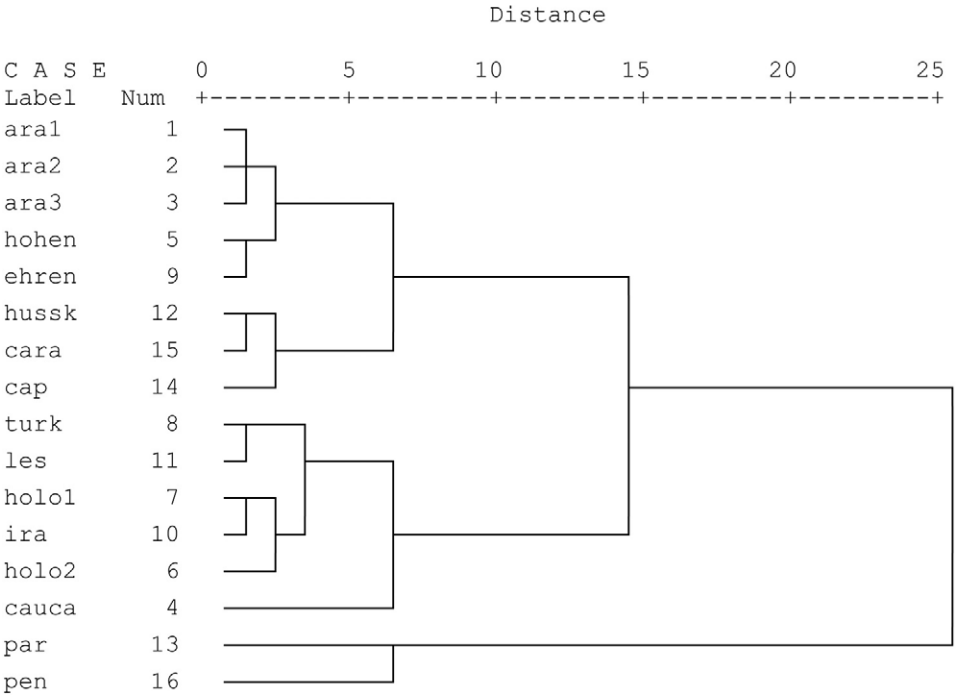

Fig. 2. UPGMA clustering of *Stipa* species studied. ara 1–3 – *St. arabica* Meshkinshahr, Tehran and Meiyaneh respectively, hohen – *St. hohenackeriana* Meshkinshahr, ehren – *St. ehrenbergiana* Meiyaneh, hussk – *St. haussknechtii* Isfahan, cara – *St. caragana* Firoozkooh, cap – *St. capensis* Loshan, turk – *St. turkestanica* Tehran, les – *St. lessingiana* Tehran, holo 1–2 – *St. holosericea* Damavand and Meiyaneh respectively, ira – *St. iranica* Tehran, cauca – *St. cacausica* Dasht, par – *St. parviflora* Mahallat, pen – *St. pennata* Dasht.

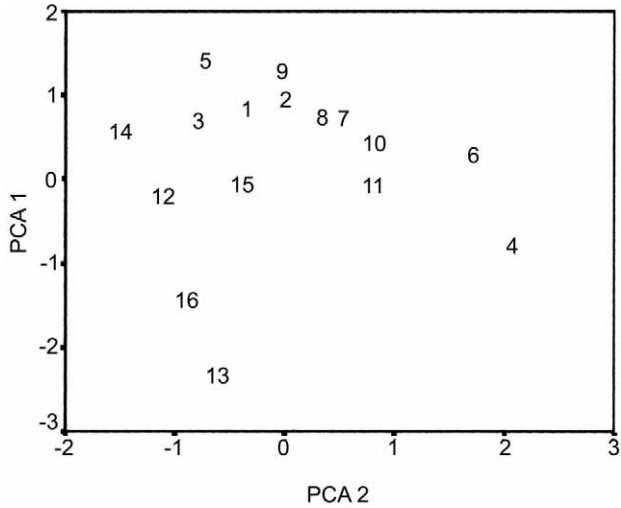

Fig. 3. PCA ordination of *Stipa* species studied. Species numbers as in Fig. 2.

The second sub-cluster is composed of *St. caragana* and *St. haussknechtii* of the sec. *Lasiagrostis* as suggested by FREITAG (1985); however *St. capensis* of sec. *Stipella* is also placed in this sub-cluster.

Two species of *St. turkestanica* and *St. lesseingiana* of the sec. *Stipa*, species group 1 (Eriostipa, FREITAG 1985) show similarity to each other and are placed in the second major cluster (Fig. 2). *St. caucasica* of the same section but from species group 2 (Brevigeniculata) shows some similarity to these two species and is joined with some distance to them supporting the FREITAG (1985) taxonomic treatment of the genus *Stipa*. However *St. pennata*, which also belongs to the sec. *Stipa*, stands somewhat distant from these species.

Two species of *St. iranica* and *St. holosericea* of the sec. *Barbatae* show similarity in meiotic characteristics and are placed together in the second major cluster as suggested by FREITAG (1985) based on morphological characteristics. Two species of *St. parviflora* and *St. pennata* stand apart from the other species due to their cytogenetic differences. PCA ordination of the *Stipa* species studied (Fig. 3) also supports the FREITAG (1985) taxonomic treatment of the genus *Stipa* in most of the cases.

Meiotic abnormalities

The meiotic irregularities observed in *Stipa* 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 and cytomoxis, which are discussed bellow.

Anaphase laggard chromosomes

Data with regard to laggard chromosomes is provided in Table 2. Some of the species showed laggard chromosomes in anaphase-I and II while the others showed a normal segregation of chromosomes during anaphase. Meshkinshahr population of *St. arabica* showed the highest percentage of anaphase-I and anaphase-II laggard chromosomes (11.42 and 2.56).

No significant negative correlation was obtained between pollen fertility and the anaphase laggard chromosomes. Therefore these meiotic abnormalities do not bring about pollen sterility. 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 I and II stages, but that genetic factors may also bring about pollen sterility as evidenced in different tetraploid strains of rye (HAZARIKA and REES 1967) as well as *Avena sativa* cultivars (BAPTISTA-GIACOMELLI et al. 2000). Therefore reduction in pollen fertility in the *Stipa* species studied may also be affected by genetic factors and not only by meiotic irregularities reported.

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 (Tab. 2). Chromosome bridges resulting from stickiness were observed in anaphase-I and II as well as telophase-I and II stages. The thickness of bridges observed and the number of chromosomes involved in their formation varied among different meiocytes and the species studied.

Tab. 2. Meiotic abnormalities in *Stipa* species studied. Sp – *Stipa* species (Species number as in Tab. 1), A1 – Anaphase-I cells showing laggard chromosome, ST1 – Anaphase-I cells showing stickiness, A2 – Anaphase-II cells showing laggard chromosome, ST2 – Anaphase-II cells showing stickiness, DT – Cells with varying division time, CY – Cells showing cytomixis, MN – Micronuclei, PF – Pollen fertility. All values in %.

Sp	A1	ST1	A2	ST2	DT	CY	MN	PF
1 *caragana*	2.00	0.00	0.00	0.00	0.00	5.00	0.00	99.60
2 *haussknechtii*	4.84	0.00	0.00	0.00	1.20	5.00	3.00	99.80
3 *parviflora*	0.00	0.00	0.00	0.00	1.00	7.00	3.10	98.20
4 *capensis*	1.80	0.00	0.00	0.00	0.30	6.00	0.40	98.00
5 *lessingiana*	0.00	0.00	0.00	0.00	0.00	20.00	0.00	98.89
6 *turkestanica*	2.00	2.00	0.00	0.00	1.00	20.45	0.00	84.00
7 *pennata*	0.80	0.00	0.00	0.00	0.00	7.00	0.90	99.70
8 *cacausica*	5.00	0.00	1.52	0.00	0.00	45.39	2.35	99.30
9 *arabica* 1	11.42	14.20	2.56	5.12	10.12	32.85	11.60	91.21
10 *arabica* 2	2.89	0.00	0.00	0.00	0.00	5.00	0.00	97.00
11 *arabica* 3	0.00	0.00	0.00	0.00	3.30	10.60	0.00	96.81
12 *hohenackeriana*	2.00	0.00	0.00	0.00	0.00	22.50	0.00	97.00
13 *ehrenbergiana*	0.00	0.00	0.00	0.00	3.00	25.00	0.00	98.85
14 *iranica*	0.00	0.00	0.00	0.00	2.00	38.45	0.00	97.36
15 *holosericea* 1	0.00	6.00	0.00	3.30	0.00	41.00	3.50	99.32
16 *holosericea* 2	0.00	0.00	0.00	0.00	1.25	25.00	0.00	99.85

Genetic as well as environmental factors have generally been considered the reason for chromosome stickiness in different plant species (NIRMALA and RAO 1996). However BAPTISTA-GIACOMELLI et al. (2000), reported a difference in the percentage of cells showing stickiness in Brazilian *Avena sativa* cultivars and suggested a genomic-environmental interaction as the main reason for the occurrence of chromosome stickiness, which may hold true for the *Stipa* species studied.

Cytomixis

Chromatin /chromosome migration occurred in different directions from early prophase to telophase-II in the *Stipa* species and populations studied (Tab. 2., Fig. 1 d). Several metaphase/ diakinesis cells in these species possessed extra or missing chromosomes showing aneuploid condition (Fig. 1 e). A particular kind of cytomixis was observed in the Sohanak population of *St. iranica* leading to the migration of the whole chromosome complement and the production of unreduced (2n) meiocytes.

Migration of chromatin material among the adjacent meiocytes occurs through cytoplasmic connections originating 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-meiocyte connections or cytomictic channels that permit

the transfer of chromosomes (FALISTOCCO et al. 1995). Cytomixis is considered to be of less evolutionary importance but it may lead to the production of aneuploid plants with certain morphological characteristics (SHEIDAI et al. 1993) or produce unreduced gametes as reported in several grass species including *Dactylis* (DÍAZ LIFANTE et al. 1992) and *Aegilops* (SHEIDAI et al. 2002). Unreduced gamete formation is of evolutionary importance leading to the production of plants with higher ploidy levels. Cytomixis by producing aneuploid pollen grains may also be responsible for reduction in pollen fertility of the *Stipa* species studied

Unreduced (2n) pollen grains

The occurrence of large pollen grains (possibly 2n pollen grains) with a frequency of 0.3–19% was observed in Sohanak population of *St. iranica*, Meyaneh population of St. *holosericea*, *St. haussknechtii*, *St. parviflora* and *St. caragana* along with smaller (normal) pollen grains. The diameter of 2n pollen grains ranged from 41.00–60.00 µm while diameter of the normal pollen grains was 28–39 in different *Stipa* species studied. T-test analysis revealed a significant difference ($p < 0.05$) in the size of unreduced pollen grains as compared to that of reduced pollen grains.

A numerically unreduced diploid, or 2n gamete is a meiotic product that bears the sporophytic rather than the gametophytic chromosome number. Such gametes result from abnormalities during either microsprogenesis (2n pollen) or megasporogenesis (2n eggs). Unreduced gametes are known to produce individuals with higher ploidy level through a process known as sexual polyploidization (VILLEUX 1985). According to HARLAN and DE WET (1975) sexual polyploidization is the major route to the formation of naturally occurring polyploids.

Different methods have been used to detect 2n gametes including morphological, flow cytometery and cytological methods. The most direct method of screening for 2n pollen involves the examination of the range of size of pollens produced by an individual, as with increase in DNA content the cell volume increases which in turn influence the pollen diameter (BRETAGNOLLE and THOMSON 1995). The presence of giant grains has been used as an indication of the production of 2n pollen (VORSA and BINGHAM 1979).

As stated earlier the frequency of 2n pollen grains varied in different *Stipa* species studied for example it was 0.3% in *St. capensis*, 6% in the Sohanak population of *St. iranica* and 19% in the Meyaneh population of *St. holosericea*. A high intra-population, inter-specific and inter-subspecific variability in the frequency of 2n pollen grain formation has been also reported in *Solanum* and *Dactylis* (BRETAGNOLLE and THOMSON 1995).

Different cytological mechanisms are responsible for the production of 2n gametes including premiotic doubling of the chromosomes, omission of the first and second meiotic division, as well as post meiotic division, occurrence of abnormal spindle geometry, abnormal cytokinesis and desynapsis (BRETAGNOLLE and THOMSON 1995).

Detailed cytological study of *St. iranica* showed the occurrence of cytomixis (discussed before) as the possible mechanism for the formation of aneuploid and 2n meiocytes, the latter might produce unreduced pollen in this species. In the other *Stipa* species producing potential unreduced pollen grains along with cytomixis, anaphase-I and II failure (Fig. 1 f) is responsible for 2n pollen grains formation. To our knowledge this is the first report of 2n pollen in *Stipa*.

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