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Meiotic behaviour, karyotype analyses and pollen viability in species of *Tamarix* (*Tamaricaceae*)

Abstract

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This study elucidates cytological aspects of the complex genus *Tamarix* (*Tamaricaceae*). Chromosome counts were performed and meiotic behaviour recorded on 30 accessions belonging to 15 taxa and three putative hybrids from different parts of Iran. Karyotype data were analysed in five species. Both gametic and somatic chromosome counts showed most species are diploid (n = 12 and $2n$ = 24), but polyploidy (n = 24 and $2n$ = 36) was found in six taxa. All the studied species showed predominance of submetacentric chromosomes and a lower proportion of metacentric pairs. The chromosomes in studied species were found to be small with a mean chromosome length of 1.05 to 2.8 µm. Karyotype analyses showed different formulas from 12sm to 7m + 5sm. Pollen viability in most species was more than 79 %, with low viability (28.5 %) observed only in *T.* cf. *kermanensis*, as a triploid taxon. This study reveals that polyploidy and hybridization could be important reasons for taxonomic complexity in *Tamarix*. Hybridization and the high chance of establishing hybrids by vegetative reproduction are major adaptive mechanisms in the successful growing, dispersal and probable rapid evolution of this genus in its native range. Furthermore these mechanisms could facilitate the spreading of *Tamarix* species outside their native range as aggressive invasive plants.

Additional key words: *Caryophyllales*, flora of Iran, hybridization, invasive plants, polyploidy, taxonomic complexity

Introduction

Tamaricaceae (*Caryophyllales*) include about 80 halophyte, rheophyte and xerophyte species occurring in arid and semi-arid zones of Asia, Africa and Europe, with a major centre in SW and C Asia (Baum 1978, Gaskin 2003a). *Tamarix*, with c. 60 species, is the largest genus in the family, with the majority of its species known from Iran and Pakistan (Baum 1978; Qaiser 1976; Akhani 2006). *Tamarix* species are shrubs and trees, and the most important diagnostic characters include the mode of leaf insertion on the stem and the configuration of the androecium, e.g. the number of stamens and the staminal disk (Baum 1978; Gaskin 2003a). *Tamarix* is one of the most taxonomically challenging genera among angiosperms, because some morphological characters have intermediate states (Baum 1978; Gaskin 2003b). Baum (1978) classified *Tamarix* into three sections and nine series, but according to Gaskin and Schaal (2003), sectional classification was not confirmed by molecular studies. Preliminary molecular phylogenetic investigation of U.S. invasive *Tamarix* has supported earlier hypothesis of hybridization in *Tamarix* species by Rusanovich (1986) (Gaskin and Schaal 2002, 2003; Gaskin and Shafroth 2005). However, the number of species and degree of hybridization are questionable and no cyto-

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logical evidence of hybridization is yet known (Smeins 2003).

In a multidisciplinary project we studied all Iranian species of the genus *Tamarix*, using morphological, cytological, anatomical and molecular methods, in order to: (1) provide a new assessment of the taxonomy of the genus based on morpho-molecular studies; (2) look for possible hybridization, and determine the degree and level of polyploidy in natural populations of Iranian *Tamarix*; and (3) search for factors responsible for diversification of the genus. Therefore, we made extensive field studies and sampling covering most parts of Iran. We have sampled our plants for morphological, molecular, anatomical and cytological studies. The molecular study will be reported in a forthcoming paper (Akhani & Borsch, in prep.).

The present paper aims to report part of the project, i.e. on the cytological aspects of *Tamarix*. Cytological investigations on several Iranian species were performed based on 30 accessions belonging to 15 taxa and three putative hybrids. In spite of our efforts to conduct meiotic and mitotic studies on all Iranian species, we were only able to obtain reliable results for almost half of them.

Materials and methods

Plant collection and identification — All species were collected in the field in their natural habitats from different parts of Iran. Voucher specimens are deposited in the Halophytes and C4 Plants Research Laboratory, School of Biology, University of Tehran (herb. Akhani), partly with duplicates in the herbarium of the Botanischer Garten und Botanisches Museum, Berlin-Dahlem (B) (Table 1).

Identification mostly follows Baum (1978). However, we have changed species delimitation and the circumscription of some taxa based on our own ongoing studies on this group with the following explanations:

1 – *Tamarix arceuthoides* Bunge is treated in this paper in a broad sense including *T. karakalensis* Freyn, *T.*

Table 1. Chromosome numbers, pollen viability, localities and collectors of *Tamarix* taxa studied in this paper. Collectors: A = H. Akhani; S = N. Samadi; N = A. R. Noormohammadi.

Taxon	*n*	2*n*	Pollen viability	Locality, Collector(s)	Voucher No.
T. androssowii Litv.	–	24	88 %	Semnan, S, N	22151
T. sp. (*T. androssowii* × *T. pycnocarpa*)	24	–	83.2 %	Kerman, A, S, N	22272
T. aphylla (L.) H. Karst	–	24	79.3 %	Kerman, A, S, N	22008
T. arceuthoides Bunge	12	–	–	Golestan, A, S	21443
T. arceuthoides	12	–	–	Golestan, A, S.	21445
T. arceuthoides	12	–	–	Golestan, A, S	21453
T. arceuthoides	12	–	88.2 %	Semnan, A, S	21572
T. arceuthoides	12	–	89 %	Semnan, A, S	21573
T. arceuthoides	12	–	96 %	Semnan, A, S	21575
T. arceuthoides	12	–	–	Khuzestan, A, S, N	21780
T. dioica Roxb. ex Roth	12	24	92 %	Sistan va Baluchestan, A, S, N	22109
T. dubia Bunge	12	–	96.8 %	Kerman, A, S, N	21970
T. cf. *indica* Willd.	12	24	79 %	Khuzestan, A, S, N	21963
T. cf. *indica*	24	–	93 %	Kerman, A, S, N	22017
T. cf. *kermanensis* B. R. Baum	–	36	28.5 %	Hormozgan, A	21670
T. cf. *kermanensis*	24	–	–	Kerman, A, S, N	22245
T. kotschyi Bunge	12	–	79.3 %	Khuzestan, A, S, N	21865
T. mascatensis Bunge	12	–	–	Khuzestan, A, S, N	21722
T. mascatensis	–	24	81 %	Sistan va Baluchestan, A, S, N	22101
T. meyeri Boiss.	12	–	99.7 %	Khuzestan, A, S, N	21720
T. octandra Bunge	–	24	–	West Azerbaijan, A, S, N	22845
T. pycnocarpa DC.	–	24	–	Hormozgan, A	21679
T. pycnocarpa	12	–	85.3 %	Khuzestan, A, S, N	21767
T. sp. (*T. pycnocarpa* × *T.* sp.)	24	–	84.2 %	Yazd, A, S, N	21967
T. ramosissimma Ledeb.	12	–	94.6 %	Golestan, A, S	21441
T. ramosissimma	12	–	–	Semnan, A, S	21542
T. ramosissimma	–	24	–	Tehran, N	22125
T. sp. (*T.* cf. *ramosissima* × *T.* sp.)	24	–	96.7 %	Esfahan, A	21381
T. stricta Boiss.	–	24	–	Hormozgan, A	21698
T. szowitsiana Bunge	24	–	93 %	Fars, A, S, N	22279

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Table 2. Total chromosome length (TCL), mean chromosome length (CL), mean arm ratio (AR), karyotype formula (KF), intrachromosomal asymmetry index (A1), interchromosomal asymmetry index (A2), Stebbins asymmetry categories (Steb.) and standard error (SE).

Taxon	TCL ± SE	CL ± SE	AR ± SE	KF	A1	A2	Steb.
Tamarix aphylla	19.74 ± 0.28	1.65 ± 0.03	1.89 ± 0.21	2m + 10sm	0.43	0.17	2A
Tamarix dioica	23.64 ± 0.44	1.97 ± 0.07	1.97 ± 0.21	12sm	0.47	0.22	2B
Tamarix cf. *indica*	18.55 ± 0.32	1.55 ± 0.06	1.90 ± 0.18	3m + 9sm	0.43	0.20	2B
Tamarix mascatensis	18.995 ± 0.28	1.58 ± 0.04	1.68 ± 0.11	7m + 5sm	0.37	0.17	1A
Tamarix stricta	21.05 ± 0.39	1.75 ± 0.04	1.95 ± 0.153	12sm	0.46	0.22	2B

korolkowii Regel & Schmalh. and *T. aralensis* Bunge following Zieliński (1994).

2 – The identity of species named *Tamarix indica* Willd. is very problematic. The reason is that the Iranian plants do not match the type specimen in the Willdenow Herbarium (B-W 06063-01 0). However, we retain Baum's interpretation by using the name *T.* cf. *indica* until the whole group is revised critically, including several taxa described from Pakistan (Qaiser 1976).

3 – *Tamarix kermanensis* B. R. Baum was described from Baluchestan Province of E Iran (Baum 1967). The two accessions showed different chromosome numbers with some differences in their morphology. We therefore prefer to name our plants under *T.* cf. *kermanensis*, until we find a chance to compare our plants with the type specimen, which was not available in the Naturhistorisches Museum Wien (W) (E. Vitek pers. comm.).

4 – Both *Tamarix aucheriana* (Decne.) B. R. Baum and *T. pycnocarpa* DC. have been described from S Iran and adjacent Iraq. Our studies support unifying these species under the older name *T. pycnocarpa*.

5 – The assigning of three putative allotetraploid taxa is based on cytological and unpublished molecular data (Akhani & Borsch, in prep.). Their parents are distinguished based on own observations in natural populations of the collected samples.

Meiotic preparation — Young racemes were fixed in Pinar solution (ethanol 96 %: chloroform: propionic acid; 6:3:2) for at least 48 h at 4°C, then were stored in 70 % ethanol at 4°C until used. Slides were prepared by squashing anthers in 2 % acetocarmine.

Mitotic preparation — For mitotic study we could not work on rootlets from germinated seeds. Furthermore, based on our limited experience, most *Tamarix* seeds quickly lose their viability (see also Horton & al. 1960). Therefore, we used propagated branchlets transferred to the laboratory. In this way we were able to successfully propagate only eight species. Somatic chromosomes were studied in root meristems pretreated in 0.05 % colchicine at room temperature for 3 h. These were then fixed in Carnoy solution (ethanol 96 %: glacial acetic acid; 3:1) for 24 h and stored in a freezer at –20°C (Sharma & Sharma 1972). Root tips were stained by hematoxylin-iron alum 4 % for 30 minutes and squashed with 45 % acetic acid (Guerra 1999). All slides were examined under a Nikon OPTOPHOT-2 and photographed by a Moticam 2300 digital camera. Karyotypic parameters were measured by MicroMeasure_3.3 (Reeves 2001) and analysed by a statistical program (SPSS version 20). The nomenclature of Levan & al. (1964) was used to determine the centromere position (the abbreviations m and sm designate metacentric and submetacentric). For the numerical characterization of karyotypes the following parameters were measured: (1) total chromosome length (TCL); (2) mean chromosome length (CL); (3) mean arm ratio (AR); and (4) karyotype formula (KF). Karyotype asymmetry was evaluated by using intrachromosomal asymmetry index (A1), interchromosomal asymmetry index (A2) (Romero Zarco 1986) and Stebbins asymmetry categories (Stebbins 1971) (see Table 2).

Pollen viability — The staining technique was used to estimate pollen viability (Dafni & Firmage 2000). Pollen was stained with cotton blue and 1000 pollen grains were counted.

Results

Meiotic behaviour

Tamarix* sp.** (T. androssowii*** Litv. × ***T. pycnocarpa*** DC.): n = 24 (Fig. 1A). The morphology and tetraploidy are congruent with our unpublished sequence data (Akhani & Borsch, in prep.), showing an allotetraploid origin. Its morphology is very similar to *T. androssowii* but its inflorescences are much more condensed, which is never seen in normal populations. Approximately 11 % quadrivalents were observed at diakinesis. Pollen viability was 83.2 %.

Tamarix arceuthoides Bunge: n = 12 (Fig. 1B, C). The chromosome count of this species is in conformity with the previous reports by Bochantseva (1972), Zhai & Li (1986) and Khatoon & Ali (1993). Some irregularity, including laggard chromosomes and a chromatid bridge, existed in anaphase I (Fig. 1C). Pollen viability varies from 88.2 % to 96 %.

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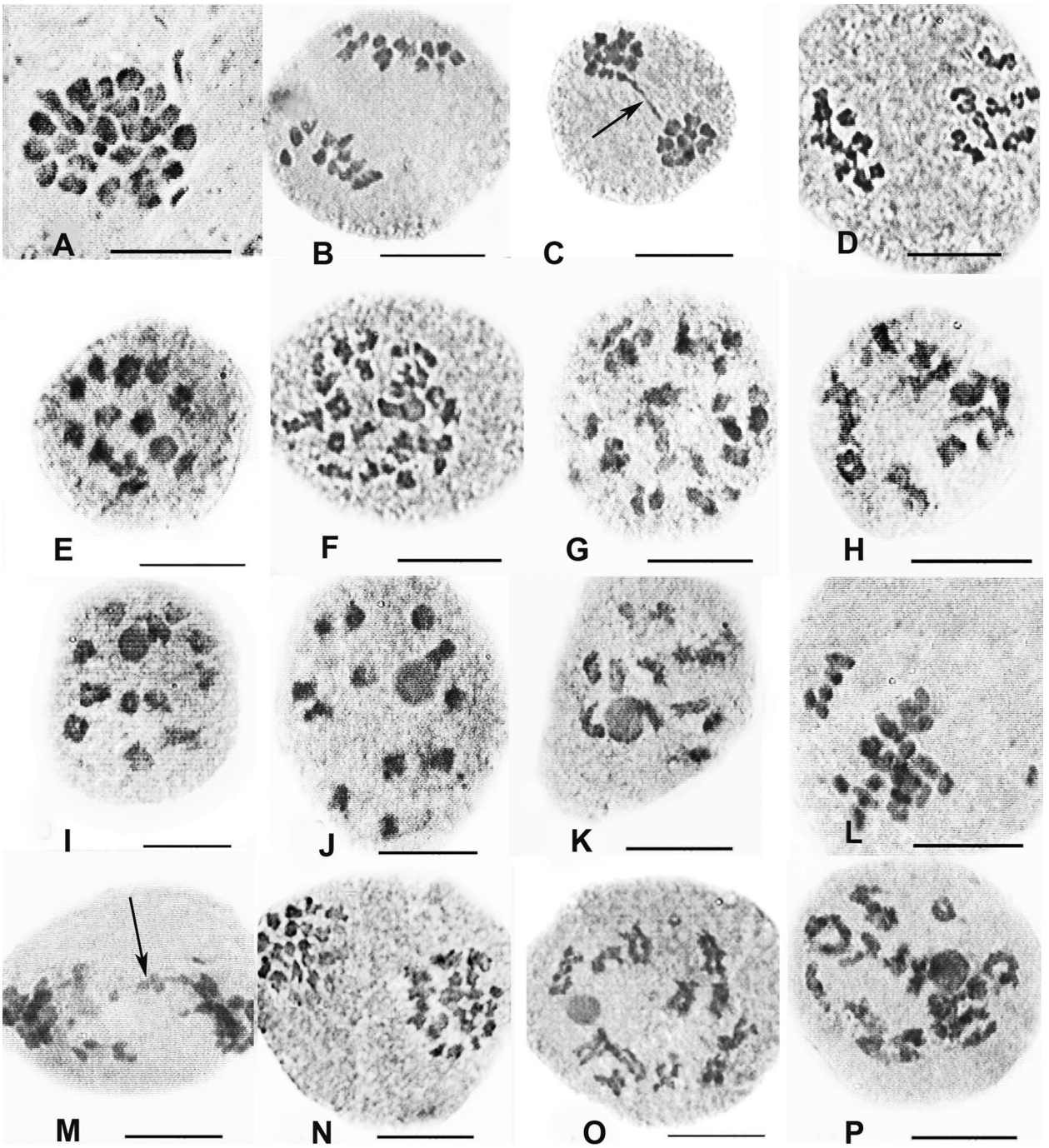

Fig. 1. Chromosome counts and meiotic analysis – A: *Tamarix* sp. (*T. androssowii* × *T. pycnocarpa*), metaphase I, *n* = 24 (22272); B: *T. arceuthoides*, anaphase I, *n* = 12 (21573); C: *T. arceuthoides*, anaphase I, arrow shows chromatid bridge (21575); D: *T. dioica*, metaphase II, *n* = 12 (22109); E: *T. dubia*, diakinesis, *n* = 12 (21970); F: *T.* cf. *indica*, diakinesis, *n* = 12 (22017); G: *T.* cf. *kermanensis*, diakinesis, *n* = 24 (22245); H: *T. kotschyi*, diakinesis, *n* = 12 (21865); I: *T. mascatensis*, diakinesis, *n* = 12 (21722); J: *T. meyeri*, diakinesis, *n* = 12 (21720); K: *T. pycnocarpa*, diakinesis, *n* = 12 (21767); L: *T.* sp. (*T. pycnocarpa* × *T.* sp.), diakinesis, *n* = 24 (21967); M: *T. pycnocarpa* × *T.* sp., anaphase I, arrow shows laggard chromosomes; N: *T.* sp. (*T.* cf. *ramosissima* × *T.* sp.), metaphase II, *n* = 24 (21381); O: *T. ramosissima*, diakinesis, *n* = 12 (21441); P: *T. szowitsiana*, diakinesis, *n* = 24 (22279). – Voucher numbers are in parentheses. Scale bar = 10 µm.

Tamarix dioica Roxb. ex Roth: *n* = 12 (Fig. 1D). This chromosome count confirms a previous report by Malik (cited in Fedorov 1974). This is the only dioecious tree among the Iranian *Tamarix* species. Meiosis was regular with 12 diads in metaphase II. Pollen viability was 92 %.

Tamarix dubia Bunge: *n* = 12 (Fig. 1E). Based on our literature survey, this is the first chromosome count for this species. Meiosis showed 12 bivalents in diakinesis and chromosome segregation was regular. Pollen viability was 96.8 %.

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Tamarix cf. ***indica*** Willd.: $n = 24$, $2n = 24$ (Fig. 1F, 2D). Chromosome counts were performed on two accessions from different parts of Iran, one wild and the other a cultivated plant. Tetraploidy ($n = 24$) was obtained at meiosis for a plant that originated from Kerman province and diploidy ($2n = 24$) was counted at metaphase of mitoses in one cultivated plant from Khuzestan province. Occasionally, in some cells, quadrivalents were observed at diakinesis. Pollen viability was 79 % and 93 %.

Tamarix cf. ***kermanensis*** B. R. Baum: $n = 24$, $2n = 36$ (Fig. 1G, 2E). One accession from Hormozgan showed triploidy counted in metaphase of mitosis, and the other from Kerman showed tetraploidy in meiosis. Pollen viability was 28.5 % in the triploid accession, the lowest viability among the studied taxa.

Tamarix kotschyi Bunge: $n = 12$, (Fig. 1H). This chromosome count supports the previous report by Bochantseva (1972). Meiosis stages show regular pairing and segregation in this species. Pollen viability was 79.3 %.

Tamarix mascatensis Bunge: $n = 12$ (Fig. 1I). According to our literature survey, this is the first chromosome count for this species. Chromosome segregation was regular in anaphase I and II and 12 bivalents were observed at diakinesis. Pollen viability was 81 %.

Tamarix meyeri Boiss.: $n = 12$ (Fig. 1J). This chromosome count agrees with the previous report by Bochantseva (1972). Chromosome pairing was regular and 12 bivalents were distinguishable at diakinesis. Pollen viability was 99.7 %.

Tamarix pycnocarpa DC.: $n = 12$ (Fig. 1K). This seems to be the first chromosome count for this species based on our literature survey. Some laggard chromosomes were observed in telophase I. Pollen viability was 85.3 %.

Tamarix* sp.** (T. pycnocarpa*** DC. × ***T.* sp.**): $n = 24$ (Fig. 1L, M). It seems that this accession represents an allopolyploid origin. This plant was collected in a population of *T. pycnocarpa*, but showed abnormality in growth form (small shrublet instead of large shrub) and 4- or 5-merous flowers with 5 or 6 stamens. The strongly amplexicaul young leaves are quite similar to *T. pycnocarpa*. The much smaller flowers and presence of tetramerous flowers suggest that its second parent might be *T. androssowii*, which occurs in the same area. Some irregularities, such as laggard chromosomes and a chromatid bridge, were observed in anaphase II and telophase II (Fig. 1M). Pollen viability was 84.2 %.

Tamarix ramosissima Ledeb.: $n = 12$, $2n = 24$ (Fig. 1O). Most of the previous reports for this species have indicated $2n = 24$ (Bochantseva 1972; Tarnavschi & Lungeanu cited in Goldblatt & Johnson 1994; Zhai & Li 1986). There is a count of $2n = 22$ according to Petrova & al. (2006), but this is not convincing because their illustration (l.c.: fig. 19) shows 23 chromosomes and one pair of chromosomes with the possibility of overlapping. In the present study this species shows regular meiosis with 12 bivalents at diakinesis and metaphase I. Chromosome segregation was detected to be regular at anaphase stages. Pollen viability was 94.6 %.

Tamarix* sp.** (T.*** cf. ***ramosissima*** Ledeb. × ***T.* sp.**): $n = 24$ (Fig. 1N). The identity of this plant is problematic. Morphologically it shows much similarity to *T. ramosissima* in its subpersistent flowers and hololophic staminal disk. The unpublished ITS sequences show multiple copies. It is probably a hybrid, although further studies are required for a reliable identification. The tetraploid accession showed 10 % quadrivalents in diakinesis. Pollen viability was 96.7 %.

Tamarix szowitsiana Bunge: $n = 24$ (Fig. 1P). This species was originally described from NW Iran (Bunge 1852). In contrast to many *Tamarix*, *T. szowitsiana* is not common in most of the places where we have seen it in the field, including the type locality. Morphologically it is very similar to *T. androssowii*, except for its relatively broader racemes and larger petals. The finding of tetraploidy in one population from Fars Province suggests that this might be an autopolyploid taxon. A previous report under this name from Turkmenistan (Bochantseva 1972) was $2n = 24$. Pollen viability was 93 %.

Karyotype analysis

Except for *Tamarix* cf. *kermanensis* ($2n = 36$), the mitotic chromosome counts of *T. aphylla*, *T. androssowii*, *T. dioica*, *T.* cf. *indica*, *T. octandra* and *T. stricta* were $2n = 24$ (Fig. 2A–E, G, H). The chromosome counts of *T.* cf. *indica*, *T.* cf. *kermanensis* and *T. stricta* are reported here for the first time, while the reports for the remaining mentioned species corroborate previous counts (Bowden 1945; Khatoon & Ali 1993; Zhai & Li 1986). The chromosomes have a small size in all investigated accessions, ranging from 1.05 to 2.8 µm. We measured the largest mean chromosome length of 1.97 µm and the largest total chromosome length of 23.64 µm in *T. dioica* (Fig. 2C). *Tamarix* cf. *indica*, with a mean chromosome length of 1.55 µm and total chromosome length of 18.55 µm, shows the smallest chromosome size among the studied accessions (Fig. 2D). According to the symmetrical categories proposed by Stebbins (1971), *T. mascatensis* belongs to category 1A, while *T. aphylla* belongs to category 2A, and *T. dioica*, *T.* cf. *indica* and *T. stricta* belong to category 2B. Romero Zarco's indices (A1, A2) are preferred for small and similar chromosomes (Oliveira & al. 2007), and based on these indices *T. dioica* and *T. stricta* with a 12 sm karyotype formula indicated the least symmetry among the accessions and *T. mascatensis* with 7m + 5sm

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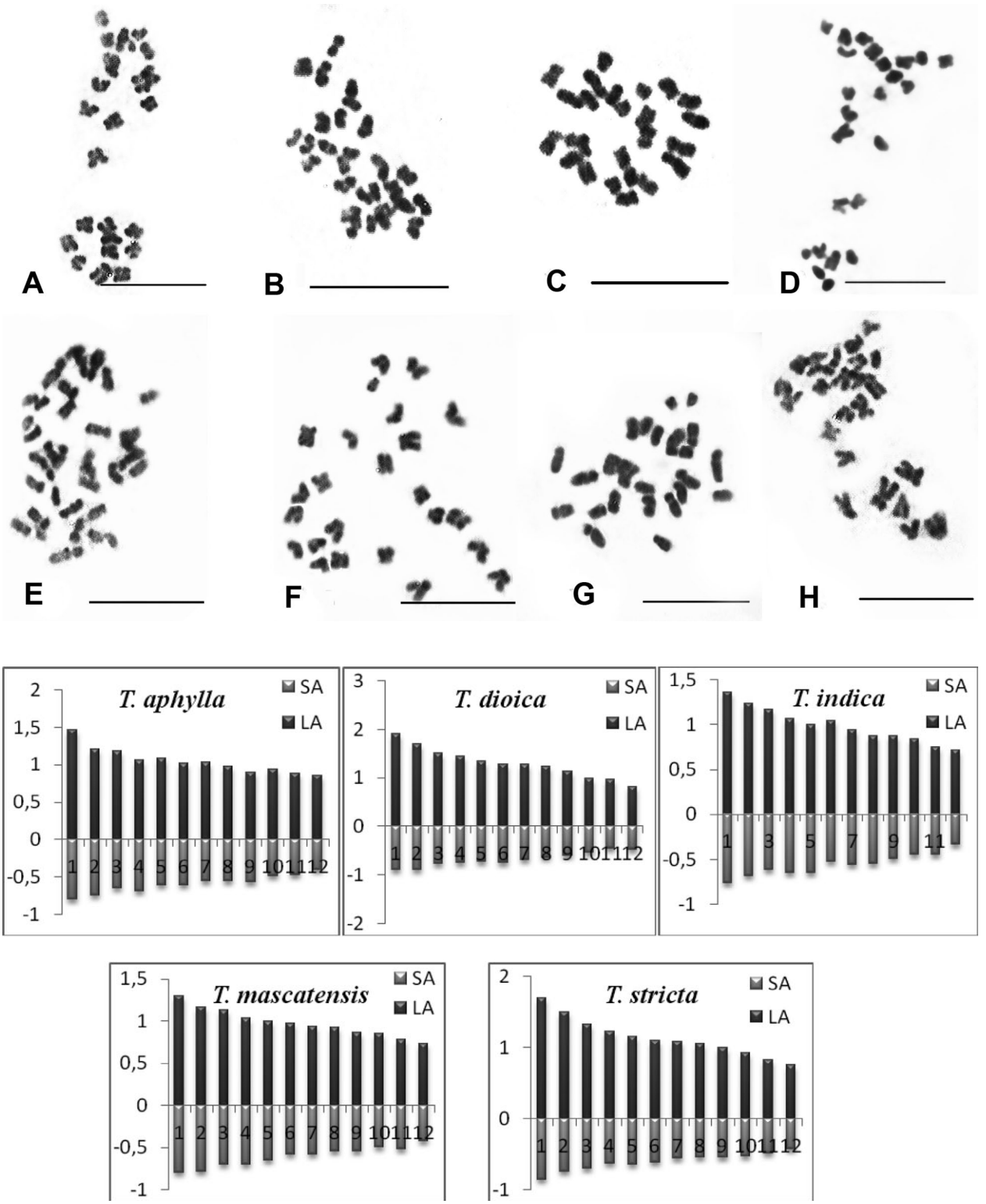

Fig. 2. Metaphase of mitosis and ideograms – A: *Tamarix aphylla*, 2*n* = 24 (22008); B: *T. androssowii*, 2*n* = 24 (22151); C: *T. dioica*, 2*n* = 24 (22109); D: *T.* cf. *indica*, 2*n* = 24 (21963); E: *T.* cf. *kermanensis*, 2*n* = 36 (21670); F: *T. mascatensis*, 2*n* = 24 (22101); G: *T. octandra*, 2*n* = 24 (22845); H: *T. stricta*, 2*n* = 24 (21698). – Voucher numbers are in parentheses. Scale bar = 10 µm. SA = short arm of chromosome; LA = Long arm of chromosome.

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was one of the most symmetrical species. The mean arm ratio ranged from 1.68 to 1.97 (Table 2). The asymmetry indices and the predominance of submetacentric and metacentric chromosomes show symmetrical karyotypes in all studied species.

Discussion

Meiotic behaviour and karyotype characteristics

Most of the analysed species showed a prevalence of submetacentric chromosomes and a lack of remarkable differences between the largest and smallest chromosomes (Table 2). Little change among asymmetry indices, arm ratio and length of chromosomes suggest neither alternation in the chromosome morphology nor great structural changes. Most of the meiotic studies showed regular chromosome pairing and segregation, but irregularities including laggard chromosomes and chromatid bridges occurred in anaphase I and II of some species (Fig. 1C, M). The constancy of karyotype characteristics and meiotic evidence could suggest that rearrangement during speciation may not have resulted in large structural mutations such as reciprocal translocations, but may have contained small or cryptic changes (Seijo & Fernández 2003).

Chromosome counts, polyploidy and hybridization

This study confirms the basic chromosome number of $x = 12$ in *Tamarix*. Different ploidy levels such as triploidy, tetraploidy and hexaploidy have been reported for *Tamarix* species so far (Bochantseva 1972). Based on this meiotic and mitotic study, most *Tamarix* species were diploid, but triploidy and tetraploidy were observed in some taxa. Different ploidy levels have been observed in *T.* cf. *kermanensis* (triploid and tetraploid) and *T.* cf. *indica* (diploid and tetraploid), probably indicating their different taxonomic status. Two different ploidy levels from *T.* cf. *kermanensis* show differences in morphological characters as well. The triploid accession showed vaginate leaves and usually synlophic disks, but the tetraploid accession was characterized by amplexicaul to pseudovaginate leaves and hololophic to paralophic disks. Different ploidy levels among the populations of the same species (cytotypes) could be one of the sources of phenotypic plasticity in these species. In addition, introgression between different accessions could play a major role in morphological diversity and consequently complicate taxonomy of the genus. Introgression between *T. canariensis*, *T. gallica* and *T. ramosissima* has been reported as a source of confusion in the characterization of some invasive *Tamarix* in the United States (Gaskin & Schaal 2003).

Polyploidization can cause morphological changes, such as the size of plant organs (Smith 1946). The most important diagnostic characters between *Tamarix androssowii* and *T. szowitsiana* are the size of the racemes and petals. The chromosome count for *T. szowitsiana* in this study ($n = 24$) suggests that it might be considered as an autopolyploid of *T. androssowii*, although, for a reliable judgment, more detailed cytological and molecular data from different populations are necessary.

Distinguishing between auto- and allopolyploids merely by cytological evidence is challenging because autopolyploids are statistically identified by presence of quadrivalent at meiosis and allopolyploids usually show bivalent at diakinesis and metaphase (Levin 2002). However, there is not general agreement on such behaviour of allopolyploids and autopolyploids (Ramsey & Schemske 2002). In this study, based on cytological and morphological data and our own unpublished molecular investigation (Akhani & Borsch, in prep.), it seems that the three tetraploid taxa, i.e. *Tamarix* sp. (*T. androssowii* × *T. pycnocarpa*), *T.* sp. (*T. pycnocarpa* × *T.* sp.) and *T.* sp. (*T.* cf. *ramosissima* × *T.* sp.), are probably hybrids. However, our field studies showed that these plants occur as unique or rare individual plants among populations of other species including their putative parents. Therefore, additional studies are required to check whether any of these taxa are well-established allopolyploid species in nature. The unpublished molecular studies on natural populations in Iran (Akhani & Borsch, in prep.) and previous molecular investigations (Gaskin 2003b; Gaskin & Schaal 2002, 2003; Gaskin & Shafroth 2005) have shown a high ability of hybridization in natural and invasive populations of *Tamarix*. Hybridization is advantageous as a potentially adaptive evolutionary factor, which can stabilize different types of variation, such as evolutionary novelty, genetic variation and fixed heterosis, and could stimulate the evolution of invasiveness (Ellstrand & Schierenbeck 2000). Hybridization and vegetative reproduction in *Tamarix* are among the biological traits of this highly invasive genus that may have led to the invasion of new ecological niches (Gaskin & Schaal 2003). Therefore, it is feasible to consider *Tamarix* as a suitable model for examining rapid evolution in the Old World arid and semi-arid areas (Whitcraft & al. 2007).

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Appendix

Detailed locality data of voucher specimens of plants studied in this paper. All specimens are deposited in the Halophytes and C4 Plants Research Laboratory, School of Biology, University of Tehran (herb. Akhani). Those indicated by "B" are represented as duplicates in the herbarium of the Botanischer Garten und Botanisches Museum Berlin-Dahlem, Freie Universität Berlin.

Tamarix androssowii Litv., Iran, Semnan: 2 km SW of Cheshmeh Ali, along seasonal river, 36°15'49.9"N, 54°04'18.8"E, 1514 m, 28 Apr 2011, *A. R. Noormohammadi & N. Samadi 22151* (B).

Tamarix sp. (*T. androssowii* Litv. × *T. pycnocarpa* DC.), Iran, Kerman: 4 km W of Sirjan, 29°23'30"N, 55°38'31"E, 1713 m, 3 Apr 2011, *H. Akhani & al. 22272* (B).

Tamarix aphylla (L.) H. Karst. Iran, Kerman: c. 3 km E of Shahdad, 30°25'02"N, 57°45'59"E, 371 m, 29 Mar 2011, *H. Akhani & al. 22008*.

Tamarix arceuthoides Bunge, Iran, Golestan: 6 km N of Gonbad towards Incheboroon, 37°19'49"N, 55°11'14"E, 51 m, 2 Jul 2010, *H. Akhani & N. Samadi 21443*; W side of Almagol wetland, near Tangoli, 37°25'N, 54°38'E, 11 m, 2 Jul 2010, *H. Akhani & N. Samadi 21453*; c. 45 km NW of Gonbad, near Fadavi village, 37°34'38"N, 54°48'46"E, 19 m, 2 Jul 2010, *H. Akhani & N. Samadi 21445*. — Semnan: 6 km W of Eyvanaky towards Tehran, 35°21'10"N, 51°59'25"E, 1041 m, 23 Oct 2010, *H. Akhani & N. Samadi 21573* & *21572* (B); 58 km SW of Sorkheh, 35°16'06"N, 52°32'48"E, 865 m, 23 Oct 2010, *H. Akhani & N. Samadi 21575*. — Khuzestan: 21 km E of Shadegan, 30°45'25"N, 48°52'06"E, 5 m, 13 Mar 2011, *H. Akhani & al. 21780* (B).

Tamarix dioica Roxb. ex Roth, Iran, Sistan va Baluchestan: c. 22 km SE of Zabol, near Mullah Ebrahim village, 30°54'39"N, 61°40'36"E, 498 m, 30 Mar 2011, *H. Akhani & al. 22109* (B).

Tamarix dubia Bunge, Iran, Kerman: 30 km NW of Anar towards Mehriz, 30°38'07"N, 55°08'30"E, 1870 m, 28 Mar 2011, *H. Akhani & al. 21970*.

Tamarix cf. *indica* Willd., Iran, Khuzestan, 20 km N of Mahshahr, Eram Park, cultivated, 30°43'N, 49°10'E, 9 m, 18 Mar 2011, *H. Akhani & al. 21963*. — Kerman: c. 12 km ENE of Shahdad, near Shojahabade Jonoobi, 30°27'24"N, 57°49'01"E, 29 Mar 2011, *H. Akhani & al. 22017*.

Tamarix cf. *kermanensis* B. R. Baum, Iran, Kerman, Fahraj, 28°58'01"N, 58°51'59"E, 664 m, 2 Apr 2011, *H. Akhani & al. 22245*. — Hormozgan: 13 km E of Bandar Abbas towards Minab, 27°17'39"N, 56°29'20"E, 6 m, 8 Mar 2011, *H. Akhani 21670*.

Tamarix kotschyi Bunge, Iran, Khuzestan: 12 km S of Aghajery towards Hendijan, dry small river bed, 30°37'50"N, 49°50'18"E, 58 m, 16 Mar 2011, *H. Akhani & al. 21865*.

Tamarix mascatensis Bunge, Iran, Khuzestan: W of Shoosh, along Karkheh river, 32°11'43"N, 48°12'45"E, 76 m, 12 Mar 2011, *H. Akhani & al. 21722*. — Sistan va Baluchestan: c. 25 km N of Zabol, East of Hamune Lake, near Shendake Barani (demolished village), along flood-preventing dam, 31°15'30"N, 61°31'54"E, 469 m, 30 Mar 2011, *H. Akhani & al. 22101* (B).

Tamarix meyeri Boiss., Iran, Khuzestan: W of Shoosh, 32°11'43"N, 48°12'45"E, 76 m, 12 Mar 2011, *H. Akhani & al. 21720* (B).

Tamarix octandra Bunge, Iran, West Azerbaijan: 7 km S of Evoghli towards Marand, along river and surrounding salty areas, 38°37'47"N, 45°15'20"E to 38°37'29"N, 45°15'07"E, 986–988 m, 6 Jun 2011, *H. Akhani & al. 22845*.

Tamarix pycnocarpa DC., Iran, Khuzestan: 26 km NW of Bostan towards Fakkeh, along Iran-Iraq border, 31°47'42"N, 47°52'23"E, 10 m, 12 Mar 2011, *H. Akhani & al. 21767* (B). — Hormozgan: c. 40 km E of Bandar Abbas, coastal saline soils near Kuleghan and border police station, 27°11'28"N, 56°37'41"E, sea level, 8 Mar 2011, *H. Akhani 21679* (B).

Tamarix sp. (*T. pycnocarpa* DC. × *T.* sp.), Iran, Yazd: between Nain and Ardakan, c. 10 km N of Aghda, 32°30'28"N, 53°33'03"E, 1170 m, 27 Mar 2011, *H. Akhani & al. 21967* (B).

Tamarix ramosissima Ledeb., Iran, Northern Khorassan Province: S border of Golestan National Park, 2 km E of Armadloo, 37°19'20"N, 56°11'52"E, 1234 m, 2 Jul 2010, *H. Akhani & N. Samadi 21441*. — Tehran: Shahriar, 1 km after Sepah square towards Tehran, along Shad-chay river, 35°41'17.4"N, 51°03'32.1"E, 1192 m, 27 Apr 2011, *A. R. Noormohammadi 22125*. — Semnan: c. 37 km NW of Damghan, near Cheshmeh Ali, 36°15'58"N, 54°04'59"E, 1527 m, 12 Oct 2010, *H. Akhani & N. Samadi 21542*.

Tamarix sp. (*T.* cf. *ramosissima* Ledeb. × *T.* sp.), Iran: Esfahan: 9 km N of Esfahan towards Kashan, 6 Jun 2010, *H. Akhani 21381*.

Tamarix stricta Boiss., Iran, Hormozgan: c. 12 km W of Rudan towards Bandar Abbas, 27°26'12"N, 57°03'33"E, 362 m, 8 Mar 2011, *H. Akhani 21698*.

Tamarix szowitsiana Bunge, Iran, Fars: 18 km W of Neyriz, near shore of Bakhtegan lake, 29°13'12"N, 54°07'28"E, 1570 m, 3 Apr 2011, *H. Akhani & al. 22279* (B).

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