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Karyological studies and chromosome variation among Iranian endemic *Allium* species (Amaryllidaceae)

Vahid Sayadi[1], Ghasem Karimzadeh[1*], Mohammad Reza Naghavi[2], and Sajad Rashidi Monfared[3]

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[1]Department of Plant Genetics and Breeding, College of Agriculture, Tarbiat Modares University, Tehran P. O. Box 14115-336, Iran

[2]Agronomy and Plant Breeding Department, Agricultural College, University of Tehran, Karaj, Iran

[3]Department of Agricultural Biotechnology, College of Agriculture, Tarbiat Modares University, Tehran P. O. Box 14115-336, Iran

[*]Corresponding author; Email: karimzadeh_g@modares.ac.ir

Abstract

One of the largest monocotyledonous genus in the Amaryllidaceae family is the *Allium* genus that includes approximately 900 species. This study aimed to examine the variations and clustering of eight Iranian endemic *Allium* species based on karyotype features. The species were collected from wild habitats across different geographical areas of Iran. *A. sativum, A. stipitatum, A. fistolosum, A. umbellicatum, A. stamineum, A. lenkoranicum,* and *A. rubellum,* were diploids ($2n = 2x = 16$), but *A. atroviolaceum* was triploid ($2n = 3x = 24$). The results represent $x = 8$ for basic chromosome numbers in all species. Analysis of variance showed significant interspecific variations for all eight chromosomal parameters tested. The mean of chromosome lengths was 11.19 μm, varied from 8.59 μm to 13.81 μm for *A. atroviolaceum* and *A. stipitatum*, respectively. In all species, the chromosome types were determined as mostly metacentric (m) and submetacentric (sm), formed five different karyotype formulas of 16m (*A. stipitatum, A. fistolosum, A. stamineum*), 14m+2sm (*A. sativum*, *A. rubellum*), 12m+4sm (*A. lenkoranicum*), 10m+6sm (*A. umbellicatum*), and 24m (*A. atroviolaceum*). According to Stebbins' classification, all karyotypes were grouped in the 1A class and represented the most symmetrical karyotypes. The information obtained from karyotype and chromosome morphology has an appreciable value in understanding the taxon evolution and interrelations.

Keywords: *Allium* L.; Chromosome; Karyotype asymmetry; Ploidy level; Variation

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Introduction

The genus *Allium* is one of the largest monocotyledonous genera in the Amaryllidaceae family that includes approximately 900 species distributed worldwide (Kusterer *et al.* 2011; Herden *et al.* 2016; Sayadi *et al*. 2020). *Allium* such as *A. cepa, A. fistulosum,* and *A. sativum* has been consumed as foods and/or spices around the world. Furthermore, *Allium* due to organosulfur composite such as allicin, plays a beneficial role in the prevention and/or treatment of different diseases (Isaacsohn *et al.* 1998; Su *et al.* 2006; Londhe *et al.* 2011; Kim *et al.* 2012). Central Asia is the main center of *Allium* diversity, while western North America is the secondary center of distribution (Etoh and Simon 2002; Garcia-Lampasona *et al.* 2003; Friesen *et al.* 2006; Jabbes *et al.* 2011). The current classifications for the genus A*llium* propose 15 subgenera and 56 sections (Friesen *et al.* 2006), almost 30 *Allium* species, containing numerous endemics growing in Iran (Wendelbo 1971). In the plant systematics,

breeding, and genetic studies, karyotypes can provide information for the identification of species and hybrid populations (Anjali and Srivastava 2012). Different ploidy levels have been reported for *Allium* as diploid ($2n = 2x = 16$), triploid ($2n = 3x = 24$), and tetraploid ($2n = 4x = 32$). The basic chromosome number of eight ($x = 8$) is dominant in most subgenera (Baranyi and Greilhuber 1999; Guetat *et al.* 2015). This study aimed to examine variations and clustering of eight Iranian endemic *Allium* species based on karyotype features.

Materials and Methods

Plant materials

The bulbs of eight different *Allium* species, including *A. sativum, A. stipitatum, A. fistolosum, A. umbellicatum, A. lenkoranicum, A. rubellum, A. stamineum*, and *A. atroviolaceum*, were collected from wild habitats across different geographical areas of Iran. The collected bulbs are being kept in the Iranian Biological Resource Center (IBRC) and used in this study. The species codes and geographical descriptions are presented in Table 1.

Chromosome analysis

Initially, intact bulbs were placed in Petri dishes and germinated on moist cotton at 20 - 25 °C in light conditions in a growth chamber. To induce and synchronize cell division, the 0.5 - 1 cm long root tips of the bulbs were first physically cold pretreated at 4 °C for 12 h and then were maintained at ambient 25 °C for 45 min. For the cytological preparations, each root tip was removed and pretreated with 0.002 M 8-hydroxyquinoline at 25 °C for 4 h in the dark to induce cell cycle delay in metaphase. The roots were washed several times in dsH_2O and fixed in 3:1 (v/v) of ethanol and glacial acetic acid (Carnoy solution) at 4 °C for 24 h. The fixed roots were washed in dsH_2O, hydrolyzed in 1 M HC1 at 60 °C for 14 min in a water bath, and washed in water, then stained by aceto-orcein 2% (w/v) at 25 °C for 2 h in darkness. Finally, for microscopic studies, the five root tips from different individuals were squashed in a drop of 45% (v/v) acetic acid and analyzed per *Allium* species. Slides were examined and microscopic photographs were taken using a light microscope (Olympus BX50; Olympus Optical Co., Ltd., Tokyo, Japan). Chromosomes were counted and its parameters were measured as long arm (L) and short arm (S) lengths, chromosome length (CL), r-value (S/L), arm ratio (AR = L/S), form percentage of chromosome ($F\% = S/\sum CL$), the total chromosome volume (TCV), and centromeric index (CI% = S/CL). TCV was measured for each species, via $\pi r^2 \times CL$, where "r" is the average radius of the chromosome cross-section. Karyotype analysis was performed via the use of MicroMeasure 3.3 computer program (Reeves 2001). The formula of Levan *et al*. (1964) was used for the karyotypic formula determination. The following parameters were used for the karyotype symmetrical evolution: TF%: total form percentage; $[(\Sigma S/\Sigma CL) \times 100]$; S%: the relative length of the shortest chromosome; RRL: range of relative length ($RL\%_{max} - RL\%_{min}$); DI: dispersion index [the ratio of centromeric gradient

(ΣS/ΣCL) ×100) concerning the CV of CL]. Accordingly, coefficient of variation of chromosome length (CV_{CL}) and Stebbins asymmetry categories was used to estimate the karyotype asymmetry. Likewise, Romero-Zarco (1986) indices: intrachromosomal asymmetry index (A1) and interchromosomal asymmetry index (A2) were calculated (Romero-Zarco 1986; Stebbins 1971; Paszko 2006; Peruzzi *et al.* 2009; Zuo and Yuan 2011; Peruzzi and Eroğlu 2013).

Statistical analyses

The experiment was carried out using a completely randomized design. Initially, assumptions of normality and homoscedasticity were verified. Then, the analysis of variance (ANOVA) was performed through the PROC GLM of SAS (SAS Institute Inc. 2009), based on the cytological data. Fisher's least significant differences method at 0.01 probability level was used for mean comparisons. Moreover, the standard errors of the means were calculated. To group the *Allium* species in this study, cluster analysis and principal component analysis (PCA) were performed based on the chromosomal parameters, using the Minitab 16 software.

Results

Among eight *Allium* species examined, seven were diploid ($2n = 2x = 16$). Interestingly, S8 with the chromosome number $2n = 3x = 24$ was triploid (Figure 1). Karyotypes and the ideograms of studied *Allium* species are presented in Figure 1 and Figure 2, respectively. ANOVA showed significant differences among the species for S, L, CL, arm ratio (AR**),** r-value, F, TCV, and CI (Table 2); their means and ranges are presented in Table 3. The mean value of CL was 11.19 μm and varied from 8.59 μm (S8) to 13.81 lm (S2). The mean TCV was 25.09 μm^3 and ranged from 14.82 μm3 (S3) to 39.45 μm3 (S2). The mean of CI% was 43% and varied from 39% (S7) to 45% (S2, S3, S8) (Table 3). The karyotype formula and symmetry information for each of the analyzed species are presented in Table 4. Karyotypes of all species were classified as class 1A of Stebbins classification (Stebbins 1971). Karyotype symmetry was presented through TF%, S%, CV_{CL}, DI, and RRL (Table 4). The maximum TF% value (45.22%) among species was obtained in the species S8 and the lowest value (39.43%) in the species S7, which shows S8 and S7 have the maximum and the minimum symmetry of the karyotype, respectively. Since a higher S% value indicates higher symmetry of the karyotype (Gennur *et al.* 2011), species S4 and species S6 with S% values of 65.17% and 50.43%, respectively had the highest symmetric and asymmetric karyotypes. The RRL values showed that species S3 with the highest RRL (8.15%) is asymmetric and the species S4 with the lowest amount of this index (5.32%) had the highest symmetrical karyotypes (Table 4). Intrachromosomal asymmetry index (A1) revealed sharp differences among the chromosome arms across different populations. A1 = 0.35 for species S7 represented the most asymmetric karyotype and species S2 and S8 had the most symmetrical karyotype among all species (A1 = 0.18). According to interchromosomal asymmetry (A2),

Table 1. Local information of studied Iranian endemic *Allium* speci

Species	IBRC* No.	Local collection sites	Latitude (N) Longitude (E)	Altitude (m)	Code in this study
A. sativum	-	Bahar, Hamadan, Iran	34° 55′ 48° 26′	1722	S1
A. stipitatum	P1010429	Mian Mil, Kermanshah, Iran	34° 36′ 47° 46′	2526	S2
A. fistulosum	-	Ghalea Now-e Ghar, Tehran, Iran	35° 50′ 51° 50′	1189	S3
A. umbilicatum	P1009439	Kangelu, Alborz, Iran	35° 50′ 51° 03′	1340	S4
A. lenkoranikum	P1008766	Chashm, Semnan, Iran	35° 57′ 53° 08′	1570	S5
A. stamineum	P1009946	Marand, Western Azarbaijan, Iran	38° 36′ 45° 47′	1543	S6
A. rubellum	P1009972	Qutor, Western Azarbaijan, Iran	38° 36′ 44° 40′	1524	S7
A. atroviolaceum	P1006775	Lavasan, Tehran, Iran	35° 48′ 51° 47′	2113	S8

*Iranian Biological Resource Center

Table 2. Analysis of variance for chromosomal parameters of studied Iranian endemic *Allium* species

S.O.V.	df	Mean squares							
		L	S	CL	AR	r-value	F%	TCV	CI%
Species	7	5.876**	3.559**	17.420**	0.078**	0.0211**	0.372**	269.30**	0.00243**
Error	32	0.370	0.188	1.058	0.002	0.0004	0.006	1.77	0.00005
CV%		9.52	9.03	9.19	2.97	2.61	1.45	5.30	1.63

**p≤ 0.01; MS: mean squares; SOV: source of variation; df: degrees of freedom; L: long arm length; S: short arm length; CL: chromosome length; AR: arm ratio; r-value: S/L; F%: form percentage of chromosome; TCV: the total chromosome volume; CI%: centromeric index

Table 3. Mean and range of chromosomal parameters in Allium species

Chromosomal parameters	Mean	Range	Species that are related to the range*	
			Low	High
S	4.80	(3.88 – 6.23)	S8	S2
L	6.39	(4.70 – 7.57)	S8	S2
CL	11.19	(8.59 – 13.81)	S8	S2
AR	1.35	(1.22 – 1.55)	S8	S7
r-value	0.75	(0.65 – 0.82)	S7	S2, S8
F%	5.37	(4.93 – 5.65)	S7	S8
TCV	25.09	(14.82 – 39.45)	S3	S2
CI	0.43	(0.39 – 0.45)	S7	S2, S3, S8

*A. sativum (S1), A. stipitatum (S2), A. fistulosum (S3), A. umbellicatum (S4), A. lenkoranicum (S5), A. stamineum (S6), A. rubellum (S7), and A. atroviolaceum (S8); S: short arm length; L: long arm length; CL: chromosome length; AR: arm ratio; r-value: S/L; F%: form percentage of chromosome; TCV: the total chromosome volume; CI%: centromeric index

Table 4. Karyotype formulas and symmetry information for each of the analyzed *Allium* species

Species*	Karyotype symmetry method				DI	TF%	S%	RRL%	CV_{CL}%
	(Levan *et al.* 1964)	(Stebbins 1971)	(Romero Zarco 1986)						
			A1	A2					
S1	7m+1sm	1A	0.26	0.20	0.08	42.53	53.94	7.27	19.89
S2	8m	1A	0.18	0.15	0.07	45.05	63.17	5.73	14.92
S3	8m	1A	0.19	0.21	0.09	44.97	51.66	8.15	21.06
S4	5m+3sm	1A	0.31	0.13	0.05	40.41	65.17	5.32	12.79
S5	6m+2sm	1A	0.27	0.16	0.07	42.39	60.77	6.11	16.18
S6	8m	1A	0.23	0.22	0.10	43.62	50.43	8.10	22.16
S7	7m+1sm	1A	0.35	0.19	0.08	39.43	56.58	7.12	19.09
S8	8m	1A	0.18	0.17	0.08	45.22	59.86	6.36	16.81

**A. sativum* (S1), *A. stipitatum* (S2), *A. fistulosum* (S3), *A. umbellicatum* (S4), *A. lenkoranicum* (S5), *A. stamineum* (S6), *A. rubellum* (S7), and *A. atroviolaceum* (S8); A1: intrachromosomal asymmetry index; A2: interchromosomal asymmetry index; DI: dispersion index; TF%: total form percentage; S%: relative length of the shortest chromosome; RRL: range of relative length; CV_{CL}: coefficient of variation of chromosome length.

species S6 and species S4 had the most symmetrical and asymmetrical karyotypes, respectively (Table 4). CV% shows the karyotype symmetry and differences among the chromosomes in a species. In a situation where a karyotype displays the high uniformity of chromosomes or in other words, the karyotype is symmetric, the value of this coefficient is low. The high CV% indicates the size distribution of chromosomes in the karyotype or, in other words, the karyotype asymmetry (Venora *et al.* 1991). Species S4 had the highest CV_{CL}% (22.16%) therefore, this species is asymmetric as compared to other species. The lowest CV_{CL}% (12.79%) belonged to species S6 that represents a symmetric karyotype among the examined species (Table 4).

Cluster analysis represented the presence of four groups (Figure 3B). The first group included three species (S1, S5, S6); the second group, only S2; the third group, two species (S3, S8); the fourth group, two species (S4, S7). The results of PCA indicated that the first two principal components accounted for 97% of the total variation. The first two components were projected in a 2-dimensional graph (Figure 3A). The first component was highly related to arm ratio [AR (L/S); - 0.98%] and the second component was strongly related to the short arm (S; - 99%).

Discussion

We studied eight *Allium* species from Iran in the current work. The analyzed *Allium* species represents $x = 8$ for basic chromosome numbers, that had previously been described for this genus (Baranyi and Greilhuber 1999; Guetat *et al.* 2015; Salmasi *et al.* 2019). All examined species, except S8, were diploid ($2n = 2x = 16$). *A. atroviolaseum* (S8) was triploid ($2n = 3x = 24$). In the present study, a new ploidy level was reported for *A. atroviolaceum.* Besides, we observed $2n = 3x = 24$ for *A. atroviolaseum*, where Miryeganeh (2011) reported the chromosome number of $2n = 2x = 16$.

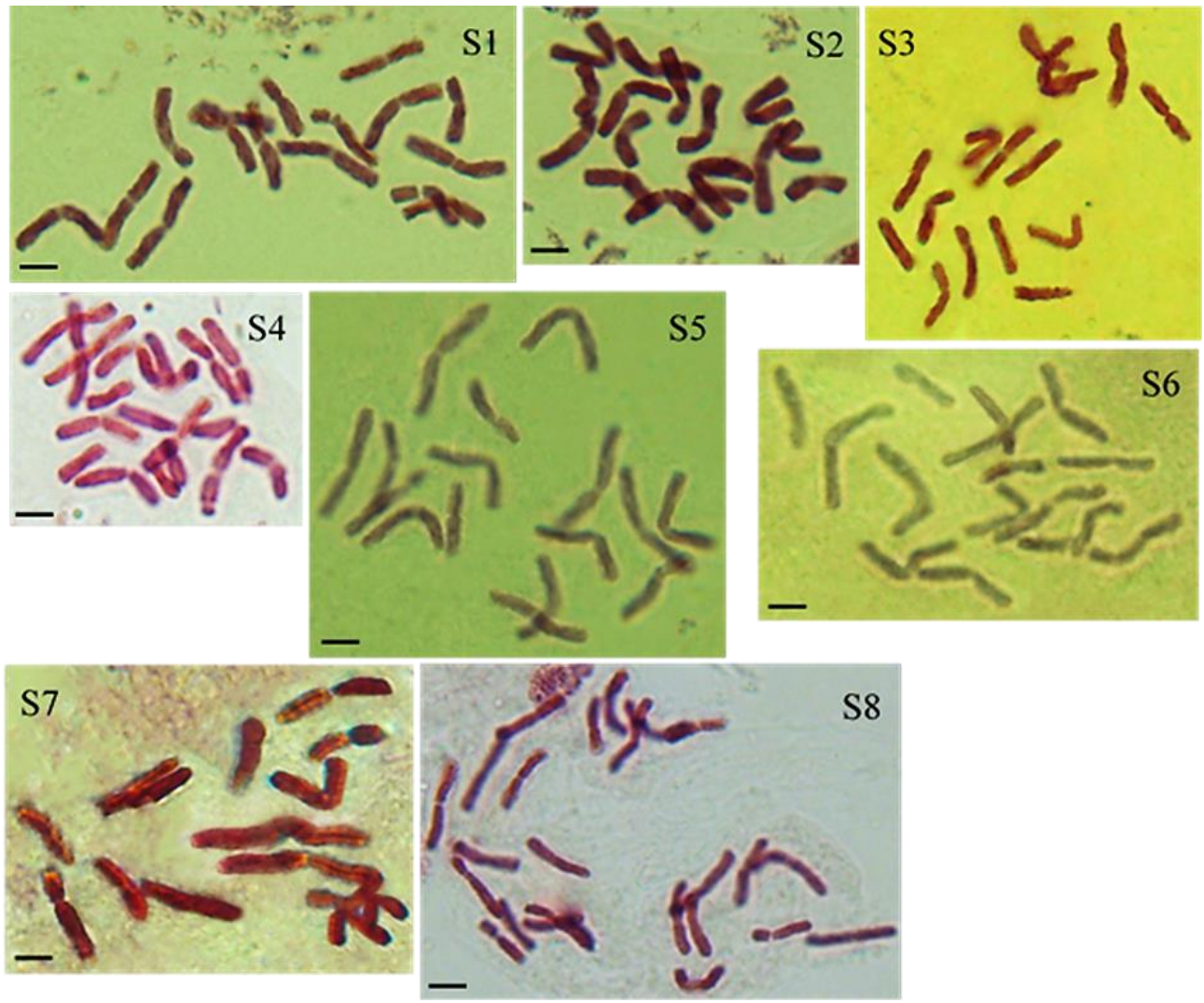

Figure 1. Somatic chromosome complements of the studied Iranian endemic *Allium* species [*A. sativum* (S1), *A. stipitatum* (S2), *A. fistulosum* (S3), *A. umbellicatum* (S4), *A. lenkoranicum* (S5), *A. stamineum* (S6), *A. rubellum* (S7), and *A. atroviolaceum* (S8)]. Scale bars = 5 μm.

Therefore, the present work offers new evidence for karyotype variation in section *Allium*; in which, variation in ploidy levels occurs (Jiemei *et al.* 1998; Zhou *et al.* 2012; Li *et al.* 2017). Different ploidy levels have been reported for *Allium* species, for instance, *A. sativum* as diploid ($2n = 2x = 16$), *A. sphaerocephalon* as triploid ($2n = 3x = 24$), and *A. porrum* ($2n = 4x = 32$) as tetraploid (Maragheh *et al.* 2019). In *Allium* genera, the diploids are more frequent and our findings are in agreement with previous reports (Paknia and Karimzadeh 2011, Salmasi *et al.* 2019). In the current work, satellites were not observed in the chromosomes in karyotypes of all studied species, while it was seen most often in other sections of the genus, are not often evident

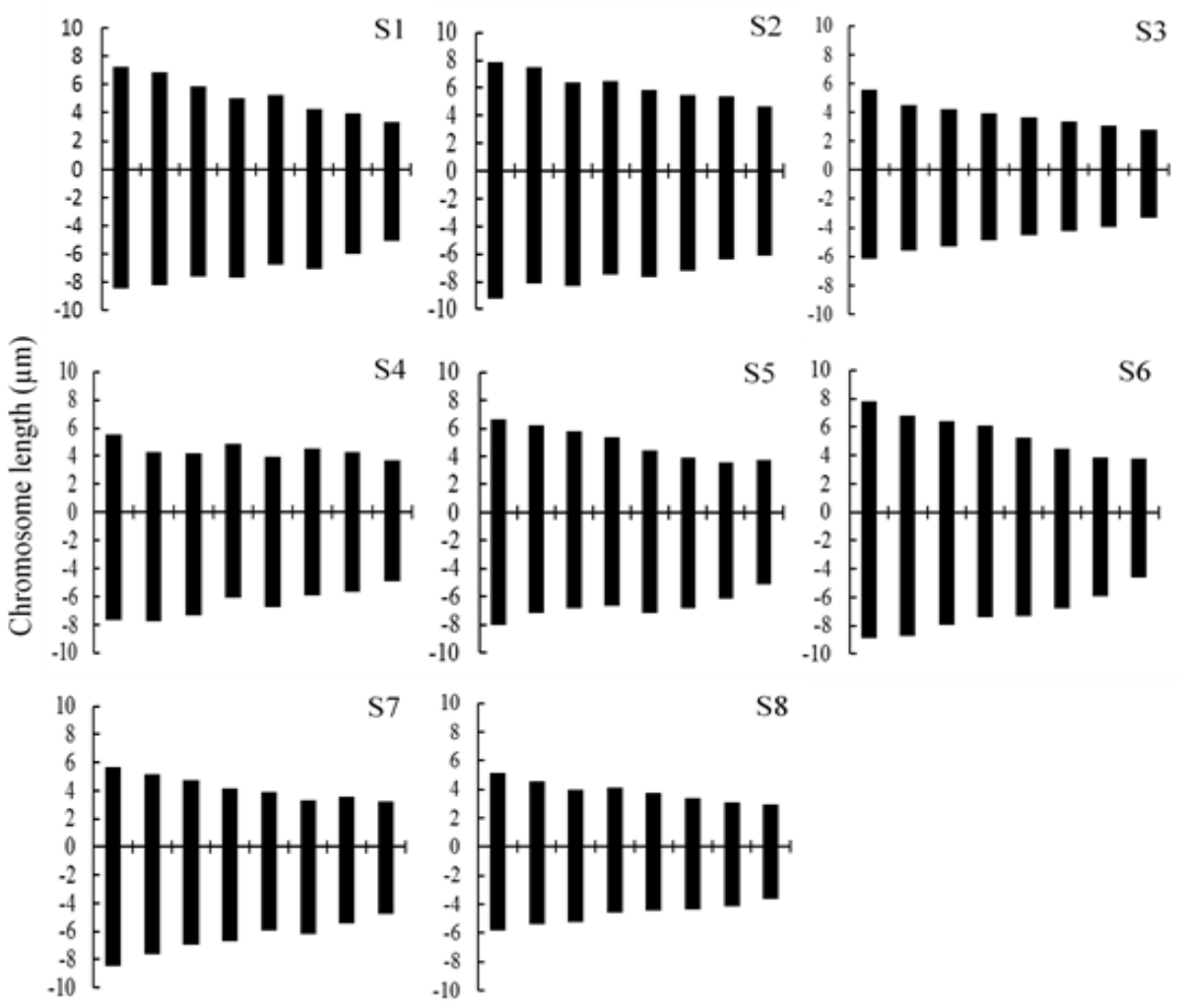

Figure 2. Idiograms of the studied Iranian endemic Allium species [A. sativum (S1), A. stipitatum (S2), A. fistulosum (S3), A. umbellicatum (S4), A. lenkoranicum (S5), A. stamineum (S6), A. rubellum (S7), and A. atroviolaceum (S8)]

in the section Allium (Fritsch and Astanova 1998). Although polyploidy occurs in various plants species and plays an essential role in the evolution of all angiosperms but the evolutionary success of a species due to the straight result of polyploidy is yet obscure (Madlung 2013). Advantages that a polyploid gets from genome doubling, allow those to grow in challenging conditions for the polyploid's diploid progenitors. The roles of triploids in species diversity have been indicated in some plant systems (Husband 2004; Chester *et al*. 2012; Miri 2020). This result

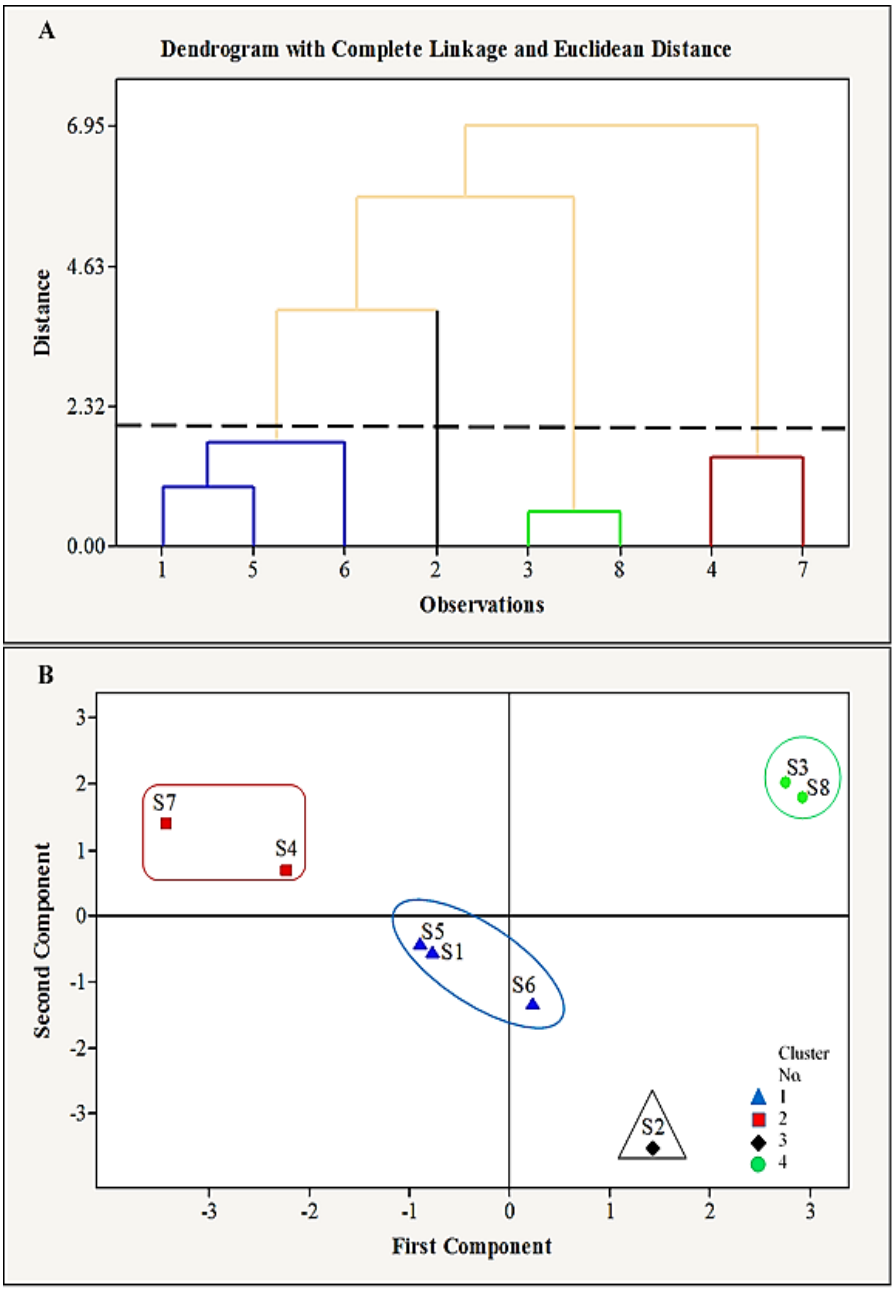

Figure 3. A) Dendrogram showing the phonetic relationships among the studied species of Allium. Constructed using the matrix of karyotype similarities and the complete linkage method (Cophenetic correlation r = 0.89). B) Diagram resulting from the principal component analysis (PCA) of the studied Allium species. The first component was highly related to arm ratio [AR (L/S); -0.98%] and the second was strongly related to the short arm (S; -99%). [A. sativum (S1), A. stipitatum (S2), A. fistulosum (S3), A. umbellicatum (S4), A. lenkoranicum (S5), A. stamineum (S6), A. rubellum (S7), and A. atroviolaceum (S8)]

proposes that they can expedite polyploid speciation. It occurs via promoting the polyploidy-diploidy coexistence or providing to genetic variation desired by neopolyploids. Accordingly, substantial occasion for divergence among *Allium* plants can be provided through chromosomal variations (Leitch and Leitch 2008; Soltis *et al*. 2014). In general, in the current study, slightly large and medium-sized chromosomes were identified in all *Allium* species examined, ranging from 8.59 to 13.81 μm. The mechanisms of karyotype differentiation could well be described via habitat variation, vegetative propagation, and polyploidization (Ao 2008). According to Stebbins' classification, all karyotypes were grouped in the 1A class. It is believed that symmetric karyotypes have a lower grade of development and evolution compared with asymmetric karyotypes (Stebbins 1971).

The PCA grouping was exactly similar to the results of cluster analysis. The results suggested that species within cluster 1 had the highest homology in chromosomal variation. For this purpose, the crossing is recommended among S1 and S5 or S6; S3 with S8, and S4 with S7, because they have the highest homology in their chromosomal characteristics. Some differences between species about karyotype formula and asymmetry indices suggest that structural changes could have helped to the genus diversity (Seijo and Fernández 2003; Karimzadeh *et al.* 2010, Karimzadeh *et al.* 2011). Cytogenetic studies as a valuable tool have been considerably carried out to investigate the phylogenetic relationships among plants, taxonomy, and diversity for many decades. The information obtained from karyotype and chromosome morphology has been of appreciable value in understanding taxon evolution and interrelations. In conclusion, although this study provided suitable information, which can be utilized in *Allium* breeding, genetics, and evolutionary studies, more studies, e.g. C-banding and FISH (Fluorescence *in situ* hybridization), are still required to clarify the details.

Conflict of Interest

The authors declare that they have no conflict of interest with any people or organization concerning the subject of the manuscript.

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مطالعه کاریولوژی و تنوع کروموزومی در گونه‌های *Allium* بومی ایران (Amaryllidaceae)

وحید صیادی[1]، قاسم کریم زاده[1*]، محمد رضا نقوی[2] و سجاد رشیدی منفرد[3]

۱ - گروه ژنتیک و به‌نژادی گیاهی، پردیس کشاورزی، دانشگاه تربیت مدرس، تهران ص پ ۳۳۶-۱۴۱۱۵
۲- گروه زراعت و اصلاح نباتات، پردیس کشاورزی و منابع طبیعی دانشگاه تهران، کرج
۳- گروه بیوتکنولوژی کشاورزی، پردیس کشاورزی، دانشگاه تربیت مدرس، تهران ص پ ۳۳۶-۱۴۱۱۵
*مسئول مکاتبه؛ Email: karimzadeh_g@modares.ac.ir

چکیده

سرده، *Allium*، با دارا بودن تقریباً ۹۰۰ گونه یکی از بزرگترین سرده‌های تک لپه‌ای در خانواده Amaryllidaceae را تشکیل می‌دهد. هدف از این مطالعه بررسی تنوع و خوشه‌بندی تعداد هشت گونه *Allium* بومی ایران بر اساس ویژگی‌های کاریوتیپی بود. گونه‌های مورد بررسی از رویشگاه‌های طبیعی آنان در مکان‌های جغرافیایی مختلف ایران جمع آوری شدند. نتایج نشان داد که گونه‌های *A. sativum*، *A. stipitatum*، *A. fistolosum*، *A. umbellicatum*، *A. stamineum*، *A. lenkoranicum* و *A. rubellum* دیپلوئید هستند (۱۶ = ۲x = ۲n)، ولی گونه *A. atroviolaceum* تریپلوئید (۲۴ = ۳x = ۲n) بود. بر اساس نتایج به دست آمده تعداد کروموزوم پایه در همه گونه‌ها برابر با ۸ = x بود. نتایج تجزیه واریانس نشان داد که تنوع بین گونه‌ای معنی‌داری برای هشت ویژگی کروموزومی مورد بررسی وجود دارد. میانگین طول کروموزوم‌ها μm ۱۱/۱۹ بود که از ۸/۵۹ μm تا ۱۳/۸۱ μm به ترتیب در دو گونه *A. atroviolaceum* و *A. stipitatum* متغیر بود. در همه گونه‌ها، نوع کروموزوم‌ها به صورت متاسنتریک (m) و ساب متاسنتریک (sm) بودند به طوری که تشکیل پنج فرمول مختلف کاریوتیپی شامل: ۱۶m (*A. stipitatum*, *A. fistolosum*, *A. stamineum*)، ۱۴m+۲sm (*A. sativum*, *A. rubellum*)، ۱۲m+۴sm (*A. lenkoranicum*)، ۱۰m+۶sm (*A. umbellicatum*) و ۲۴sm (*A. atroviolaceum*) دادند. بر مبنای دسته‌بندی استبینز، همه کاریوتیپ‌ها در کلاس ۱A گروه بندی شدند که نشان دهنده متقارن ترین کاریوتیپ‌ها می‌باشد. اطلاعات به دست آمده از کاریوتیپ و ریخت‌شناسی کروموزوم در درک تکامل تاکسون و روابط متقابل بین آن‌ها از اهمیت بالایی برخوردار است.

واژه‌های کلیدی: تقارن کاریوتیپی؛ کروموزوم؛ تنوع؛ سطح پلوئیدی؛ *Allium* L.