

POLYPLOIDY AND B CHROMOSOMES IN *ALLIUM FLAVUM* FROM SERBIA

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Abstract - The most intriguing karyological features of the genus *Allium* are polyploidy and the frequent appearance of supernumerary or B chromosomes (Bs). Specimens of *Allium flavum* from natural populations at the Gornjačka Gorge in the vicinity of Gornjak Monastery, Serbia, were analyzed karyologically. All studied plants were tetraploid ($2n = 32$). One submetacentric B chromosome representing 1% of the genome, smaller than the smallest chromosomes of the standard set, was present in some plants. This is the first finding of Bs in tetraploid *A. flavum*.

Key words: *Allium flavum*, B chromosomes, tetraploids

INTRODUCTION

Being the largest in the family Amaryllidaceae, the genus *Allium* comprises more than 800 species of perennial, mostly bulbous plants (Fritsch et al., 2010). These are mainly distributed in subtropical and temperate regions of the Northern Hemisphere, particularly around the Mediterranean region and in Central Asia. Although favourable cytological characteristics make species from the genus *Allium* attractive subjects for study, chromosome numbers are known for only about one-third of them and detailed cytological data are very limited. The most intriguing karyological features of the genus *Allium* are polyploidy and the frequent appearance of B chromosomes (Bs). Up to now, Bs have been found in 97 species (Table 1). Different levels of ploidy are also frequent, and in ten species Bs are present in polyploids as well.

Bs are supernumerary components of the genomes of numerous species of plants, fungi and animals. The term B chromosome was first used by Randolph (1928) to describe supernumerary or extra chro-

mosomes in maize, and since that time it has been applied to such chromosomes in a variety of species from all the major taxa (Jones 1995), apart from birds (Vujošević and Blagojević, 2004). It is assumed that, in general, Bs occur in about 15% of species, but the heterogeneity of different Bs poses a problem of definition, since the number of characteristics shared by all Bs is very limited. Therefore, their dispensable nature describes them the best, while the absence of recombination with any member of the basic A chromosome set and irregular, non-Mendelian modes of inheritance serve for recognising that the supernumerary chromosome is in fact a B chromosome. In general, B chromosomes are found in some members of a population, but not in others (Jones and Rees 1982). In addition, some features are common to Bs, but never shared by all of them. For instance, Bs are often smaller than chromosomes of the standard set and in plants this is true for more than half the species possessing Bs. However, Bs as large as the largest chromosomes of the set also exist. Completely heterochromatic Bs are more characteristic for animals than for plants, yet half of all Bs in plants are heterochromatic (Jones, 1975, 1995). There is a large

amount of variability between families regarding the presence of species with Bs, but part of this may be explained by differences in study intensity, as is the case with bulbous monocots being amenable to chromosome analysis.

B chromosomes were repeatedly found in *Allium flavum* (Chesmedzhiev, 1971; Šopova, 1971; Vosa, 1973; Capineri et al. 1978; Baltisberger and Baltisberger, 1995; Krahulcová, 2003) but always in diploid specimens. Here, for the first time, we present the appearance of Bs in tetraploid specimens of *Allium flavum*.

MATERIALS AND METHODS

Specimens of *Allium flavum* were collected from natural populations at Gornjačka Gorge near the Gornjak Monastery (East Serbia). Actively growing roots of about 1-1.5 cm in length were excised, treated with 0.02% colchicine for 5 h, kept in Carnoy's fixative overnight, hydrolyzed in 1 N HCl at 60°C for 12 min, stained with aceto-orcein, and squashed. Slides were analyzed using a Zeiss Axio Observer.Z1 light microscope (1600x), and the number of chromosomes was counted. Chromosome counts were made from at least five root tips of each plant.

The length of the chromosomes was measured in micrometers (μm) from images, using MicroMeasure 3.3 (<http://www.colostate.edu/Depts/Biology/MicroMeasure/>). Centromere positions were recorded. In addition, the relative size (percentage of each chromosome within the total length of the complement) and centromere index (ratio between the length of the short arm and the total chromosome length) were scored for each chromosome. The nomenclature of chromosomes in the basic set was followed according to Levan et al. (1964), and chromosomes were named as 1, 2, 3, 4, 5, 6, 7 and 8 in descending order of length.

RESULTS AND DISCUSSION

The karyotype of *Allium flavum* contained four haploid chromosome sets ($2n = 32$, FN = 64). B chromo-

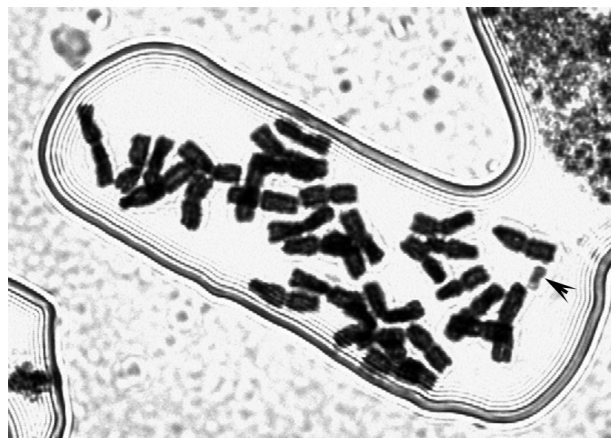


Fig. 1. Tetraploid mitosis in *Allium flavum* with one B chromosome (arrow).

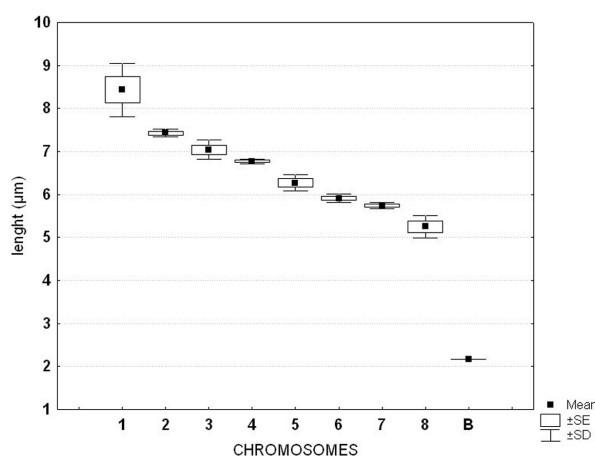


Fig. 2. Average length of chromosomes in tetraploid *Allium flavum* determined by MicroMeasure 3.3.

somes were detected in some plants (Fig. 1). Most chromosomes were large, and the karyotype analysis revealed a dominance of metacentrics. Centromeric indexes varied from 0.459 to 0.474. Chromosome length ranged from 8.44 μm for chromosome 1 to 5.25 μm for chromosome 8 (Fig. 2). B chromosomes represented approximately 1% of the tetraploid genome and were less than half the size of the smallest chromosome in the karyotype. They were sub-metacentric with centromeric index 0.395.

Allium flavum occurs in Europe in both diploid and tetraploid forms. Besides a constant dip-

Table 1. Species with B chromosomes in the genus *Allium*.

	Species	Ploidy	2n	Number of Bs	Reference
1.	<i>A. albidum</i>	2x	16	4	Cheshmedzhiev (1975)
2.	<i>A. alexeianum</i>	2x	16	2, 4	Pogosian & Seisums (1992)
3.	<i>A. allegheniense</i>	2x	14	0-4	Levan (1932)
4.	<i>A. ameloprasum</i>	3x	24	1-2	Kollman (1971, 1972)
		4x	32	1	Kollman (1972)
	<i>ameloprasum</i> group	4x	32	2-4	Bohanec et al. (2005)
5.	<i>A. angulosum</i>	2x	16	0-3	Levan (1934), Šopova (1966), Měsíček (1992)
		4x	32	2	Dmitrieva (2000)
		4x	32	0-1	Šopova (1966)
6.	<i>A. anisopodium</i>	2x	16	0-1	Frizen (1983), Tolgor et al (1994)
7.	<i>A. arvense</i>	2x	16	0-2	Marcucci & Tornadore (1997)
8.	<i>A. ascalonicum</i>	2x	16	1	Bartolo et al. (1984)
9.	<i>A. barszczewskii</i>	4x	32	1	De Sarker et al (1997)
10.	<i>A. barthianum</i>	2x	16	3	Hamoud et al (1990)
11.	<i>A. bidentatum</i>	4x	32	1	Tolgor et al (1994)
12.	<i>A. bimetrace</i>	2x	16	0-4	Bothmer (1970)
13.	<i>A. bourgeaui</i>	2x	16	0-1	Bothmer (1975)
14.	<i>A. brulloi</i>	2x	16	1	Salmeri (1998)
15.	<i>A. calabrum</i>	2x	16	2	Brullo et al. (1994)
16.	<i>A. carinatum</i>	3x	24	0-3	Šopova (1971)
17.	<i>A. cappadocicum</i>	2x	16	1	De Sarker et al (1997), Özhatay (2002)
18.	<i>A. cardiostemon</i>	2x	16	1	Pogosain (1983), Hosseini & Go (2010)
19.	<i>A. caspium</i>	2x	16	1	Zakirova & Nafanailova (1990)
20.	<i>A. cepa</i>	2x	16	1	Noda (1953)
21.	<i>A. cernuum</i>	2x	14	0-11, 13	Grun (1959), Chinnapa & Basappa (1986)
22.	<i>A. chrysantherum</i>	2x	16	1	Koyuncu & Özhatay (1983)
23.	<i>A. cirrhosum</i>	2x	16	1	Cheshmedzhiev (1975)
24.	<i>A. commutatum</i>	2x	16	1-2	Bothmer (1982)
25.	<i>A. condensatum</i>	2x	16	1	Tolgor et al (1994)
26.	<i>A. consanguineum</i>	2x	16	0-1	Mehra & Pandita (1978)
27.	<i>A. curtum</i>	2x	16	4	Özhatay & Johnson (1996)
28.	<i>A. dalmaticum</i>	2x	16	0-2	Feinbrun (1950), Lovka (1995) Brullo et al. (1996)
29.	<i>A. dasyphyllum</i>	2x	16	0-1	Pogosian & Seisums (1992)
30.	<i>A. derderanum</i>	2x	16	1	Pogosian (1983)
31.	<i>A. dictyoprasum</i>	2x	16	0-1	Özhatay & Johnson (1996)
32.	<i>A. dictyoscordum</i>	2x	16	1	Hosseini & Go (2010)
33.	<i>A. dodecadontum</i>	2x	16	0-1	Pogosian & Seisums (1992)
34.	<i>A. ericetorum</i>	2x	16	1	Wetschnig (1995), Marcucci & Tornadore (1999)
35.	<i>A. fibrosum</i>	2x	16	0-2	Vakhtina (1989)

Table 1. Continued

	Species	Ploidy	2n	Number of Bs	Reference
36.	<i>A. flavum</i>	2x	16	1, 2	Cheshmedzhiev (1971), Baltisberger & Baltisberger (1995), Krahulcová (2003)
		4x	32	0-1	This paper
37.	<i>A. flavens</i>	2x	16	+ Bs	Loidl (1982a)
38.	<i>A. fominianum</i>	2x	16	2	Pogosian (1983)
39.	<i>A. funckiaefolium</i>	2x	16	0-5	Jing et al. (1999)
40.	<i>A. fuscoviolaceum</i>	2x	16	1	Özhatay (1993)
41.	<i>A. fuscum</i>	2x	16	0-1	Cheshmedzhiev (1975)
42.	<i>A. globosum</i>	2x	16	2	Kudryashova (1988)
43.	<i>A. gramineum</i>	2x	16	2	Pogosian (1991)
44.	<i>A. guttatum</i>	2x	16	+ Bs	Tzanoudakis (1992)
45.	<i>A. iranicum</i>	2x	32	0-1	Ghaffari (2006)
46.	<i>A. jodanthum</i>	2x	16	0-1	Ohle (1992)
47.	<i>A. kuramense</i>	2x	16	1	Fritsch et al. (1998)
48.	<i>A. laeve</i>	4x	32	2	Miryeganeh & Movafeghi (2011)
49.	<i>A. macrostemon</i>	3x	24	1	Wang et al. (2009)
50.	<i>A. mairei</i>	2x		+Bs	Chen et al. (2005)
		4x		+Bs	Chen et al. (2005)
51.	<i>A. margaritaceum</i>	2x	16	0-2	Šopova (1970), Lovka (1995)
		3x	24	0-1	Šopova (1970)
52.	<i>A. melantherum</i>	3x	24	1	Cheshmedzhiev (1979)
53.	<i>A. montanum</i>	4x	32	3	Wetschnig (1992)
54.	<i>A. moschatum</i>	2x	16	0-1	Tzanoudakis (1992)
55.	<i>A. nanodes</i>	2x	16	0-3	Jing et al. (1999)
56.	<i>A. nanum</i>	2x	16	0-1	Cheshmedzhiev (1976)
57.	<i>A. neriniflorum</i>	2x	16	0-1	Li et al. (1996)
58.	<i>A. nutans</i>	2-5x	16-40	0-1	Šopova (1966)
		?	42, 44, 68	+B	Levan (1932)
59.	<i>A. ochroleucum</i>	2x	16	0-1	Holub et al. (1970)
60.	<i>A. ovalifolium</i>	2x	16	1-6	Jing et al. (1999)
61.	<i>A. paepalanthoides</i>	2x	16	3	Zhang et al. (1993)
62.	<i>A. palestinum</i>	4x	28	1	Kollman (1973)
63.	<i>A. pallens</i>	2x	16	0-1	Loidl (1982b), Özhatay (1993), Puizina et al. (1995)
64.	<i>A. paniculatum</i>	2x	16	0-3	Ved Brat (1965), Ruiz Rejon et al. (1986)
65.	<i>A. plurifoliatum</i>	2x	16	1	Zhang et al. (1993)
66.	<i>A. polyanthum</i>	4x	32	1	Guern et al. (1991)
67.	<i>A. porrum</i>	2x	16	6	Nybm (1974)
		4x	32	0-3	Vosa (1966)
68.	<i>A. prattii</i>	2x	16	0-5	Jing et al. (1999), Xue et al. (2000)
69.	<i>A. przewalskianum</i>	2x	16	0-2	Ao (2008)

Table 1. Continued

	Species	Ploidy	2n	Number of Bs	Reference
70.	<i>A. pseudoflavum</i>	2x	16	2	Кудряшова (1988)
71.	<i>A. pulchellum</i>	2x	16	0-3	Tschermak-Woes and Schiman (1960)
72.	<i>A. ramosum</i>	2x	16	0-1	Zou & Jia (1985), Yang (2001)
73.	<i>A. rotundum</i>	2x	16	0-2	Löve (1976), De Sarker et al (1997)
		?	36-38	1	Löve (1976)
		5x	40	4	Löve (1976)
		6x	48	1	Löve (1976)
74.	<i>A. rubellum</i>	2x	16	0-1	Pogosian (1991)
75.	<i>A. rubens</i>	2x	16	0-1	Ohle (1992)
76.	<i>A. rupicola</i>	2x	16	1	Tanker & Kurucu (1979), Özhatay (2002)
77.	<i>A. schoenoprasum</i>	2x	16	0-18	Bougourd (1976)
78.	<i>A. schugnanicum</i>	2x	16	0-1	Pogosian & Seisums (1992)
79.	<i>A. scorodoprasum</i>	2x	16	0-2	Lövkvist & Hultgård (1999)
		4x	32	1	Karabokiroy (1995)
80.	<i>A. senescens</i> (= <i>A. lusitanicum</i>)	2x	16	0-5	Fernandez-Casas et al. (1978)
		4x	32	0-4	Holub et al. (1970)
81.	<i>A. sieheanum</i>	3x	24	1	Özhatay (2002)
82.	<i>A. sphaerocephalon</i>	2x	16	0-2	Bothmer (1970), Viegi & Renzoni (1981), Pastor (1982), Guillén & Rejón (1984)
83.	<i>A. stamineum</i>	2x	16	0-1	Loidl (1982a)
84.	<i>A. stracheyi</i>	2x	14	2-10	Sharma and Aiyanger (1961)
		2x	16	1	Pandita (1981)
85.	<i>A. suaveolens</i>	2x	16	0-3	Fernandes (1950)
86.	<i>A. taeniopetalum</i>	2x	16	1	Fritsch & Astanova (1998)
87.	<i>A. tardans</i>	2x	16	1	Tzanoudakis (1986)
88.	<i>A. textile</i>	2x	14	0-1	Cai and Chinnappa (1987)
89.	<i>A. thracicum</i>	3x	24	0-1	Ceschmedziev (1992)
90.	<i>A. thunbergii</i>	2x	16	0-4	Noda and Watanabe (1968)
		4x	32	0-6	Noda and Watanabe (1968), Noda & Li (1980)
		6x	48	0-4	Noda and Watanabe (1968)
91.	<i>A. tulipifolium</i>	2x	16	0-1	Frizen (1986), Frizen (1988)
92.	<i>A. ursinum</i>	2x	14	0-1	Vujošević and Blagojević (2002)
93.	<i>A. victoralis</i>	2x	16	0-5	Jing et al. (1999)
94.	<i>A. vineale</i>	2x	16	0-2	Lövkvist and Hultgård (1999)
		4x	32	1-4	Měsíček & Javůrková-Jarolímová (1992)
95.	<i>A. vodopjanovae</i>	2x	16	0-2	Frizen (1988)
96.	<i>A. wallichii</i>	2x	14	1-2	Chang et al. (2006)
97.	<i>A. webbii</i>	2x	16	4	Cheshmedzhiev (1975)

loid number $2n = 16$, the tetraploid cytotype ($2n = 32$) was found in Poland (Mizianty and Frey, 1973), Spain (Ruiz Rejón and Sañudo, 1976), Italy (Bartolo et al., 1978), Austria (Loidl, 1979), Greece (Tzanoudakis and Vosa, 1988) and Bulgaria (van Loon and van Setten, 1982). Both diploids and tetraploids have been recorded in Austria, Greece and Bulgaria. Entirely new distributions of cytotypes were noted for many plant species after wide use of flow cytometry techniques. For instance, Šafařová et al. (2011) found four cytotypes with different levels of ploidy (3x, 4x, 5x and 6x) in *Allium oleraceum*. Therefore, it would not be surprising if more cytotypes for *A. flavum* are discovered in the future, assuming that many more populations are studied.

In all earlier reports Bs were found only in diploid specimens of *A. flavum*. Thus, Šopova (1971) noted that a single B chromosome was constantly present in the frequency of 0.54 in a diploid population of *A. flavum* from mountain Galičica (FRG Macedonia). This B chromosome was easily distinguished from A chromosomes both by its morphology and size, i.e. it was shorter than the smallest chromosome of the standard set, with the centromere positioned subterminally. Moreover, the B chromosome was almost completely heterochromatic. It was also found that chiasma frequency increased in the presence of B chromosomes and that the flowering time of plants with Bs was delayed in both the natural habitat and in a botanical garden. Loidl (1982a) showed that in this species Bs have less heterochromatin than A chromosomes, but a similar C-band location. In one case, he noticed a nucleolus organizing region in a B chromosome. In the diploid *A. flavum* from Austria, Bs differ within and between populations to a great extent in both size and shape. Thus, three different types of Bs were distinguished in one population, all being submetacentrics. In the Czech Republic, Krahulcová (2003) found diploid plants with two B chromosomes, which were smaller than the other chromosomes of the set. One B chromosome was discovered in diploid plants in Albania (Baltisberger and Baltisberger 1995).

As a rule, Bs are less frequent in species with lower ploidy level. In the genus *Allium*, about 20% of species with Bs are polyploid, one third of them are triploids and the others are tetraploids. Rarely, Bs appear in penta- and hexaploids. Thus, the occurrence of Bs in tetraploid *Allium flavum* is a rare but not unexpected event.

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