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Contribution to knowledge about nuclear DNA amounts in the family Asteraceae: first assessments in one genus and 12 species, with chromosome counts for three taxa

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ABSTRACT: We present in this paper the first assessments, made by means of flow cytometry, of nuclear DNA amounts in one genus, 11 species, and one variety (including the first data from wild material in the case of one of the species), all of them from the family Asteraceae. Chromosome numbers are provided for three of these taxa, the presented material including new data for one species. These data complement existing information on plant genome size in the largest plant family.

Keywords: 2C-value, Asteraceae, Compositae, flow cytometry, nuclear DNA amount, vascular plants.

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INTRODUCTION

Genome size, i.e., the amount of nuclear DNA in living organisms, is a fundamental biological character (Bennett & Leitch 2005). When Swift (1950) proposed the term C-value to define the DNA content of the unreplicated gametic chromosome set of an individual, it was considered characteristic and invariable (the C standing for constant) for every taxon. Since then, genuine intraspecific genome size variation has often been detected (Gregory 2005; Leitch *et al.* 2013 and references therein), and several terms have been coined to represent different concepts in this field (Greilhuber *et al.* 2005). Nuclear DNA content is correlated with many biotic and abiotic characters (Bennett & Leitch 2005). Flow cytometry has shown itself to be the easiest and most productive method for assessment of nuclear DNA amounts, although other techniques, such as Feulgen microdensitometry, have been employed as well (Doležel *et al.* 2007 and references therein). Despite its relevance and the efforts of investigators to increase knowledge of this parameter by one method or another, genome size is currently known for only about 2% of angiosperms (Bennett & Leitch 2011).

The chromosome number is one of the most basic karyological and cytogenetic characters, constituting information relevant for plant systematic and evolutionary assessments (Stuessy 2009, 2011). It is a parameter that is obviously correlated with genome size, especially in polyploid taxa (Bennett & Leitch 2005). Despite the ease

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of its determination, the chromosome number has been reported for only slightly more than 25% of angiosperm taxa (Stuessy 2009) or for only 20% according to Rice *et al.* (2015).

The family Asteraceae Martinov or Compositae Giseke is the largest of plant families in terms of species number. It comprises many economically important plants, including some crops, and is one of the most cosmopolitan plant families, being abundantly present in all parts of the world except in Antarctic lands (Kadereit & Jeffrey 2007; Funk *et al.* 2009). In this family, which has been highly studied from many viewpoints, the number of species with available information about genome size information is greater than in angiosperms in general, but still only approaches 5% (Garcia *et al.* 2014). In *Artemisia* L., the Asteraceae genus with the most species studied from this viewpoint (Garcia *et al.* 2014), roughly 25% of the taxa have genome size records to date, while chromosome numbers have been reported for almost 62% of the taxa (Vallès *et al.* 2011).

Research on angiosperm genome size has often been encouraged (Bennett & Leitch 2011; Galbraith *et al.* 2011), and work on angiosperm chromosome numbers has also been seen as necessary (Stuessy 2009, 2011). With precise figures, Bennett & Leitch (2011) proposed a target of DNA amount assessment in 2,500 angiosperm species in the period 2012-2016, whereas Garcia *et al.* (2014) envisaged research on 1,200 species of the family Astereaceae in the period 2014-2018.

Following these recommendations and centring on the family Asteraceae, in this paper we set out 1) to obtain novel information about plant nuclear DNA amounts in some taxa of this family; and 2) to complement, in some cases, these genome size estimates with determination of the chromosome number in the same populations. Consistent with this, only plants with unreported nuclear DNA content (in one case, with unknown genome size in wild populations) were taken into account in the study. Chromosome counts were performed whenever possible, paying special attention to taxa in which such data are

Table 1. Provenance and life cycle of the taxa studied.

Taxon[1] (tribe)	Population and collection data (herbarium voucher)	Life cycle
Artemisia densiflora Viv. (Anthemideae)	1. Italy: Sardinia, Maddalena archipelago, Caprera island: Stagnali gulf, near Stagnali town. J. Vallès, 17/11/2015 (BCN 126584) 2. Italy: Sardinia, Maddalena archipelago, Maddalena island: Baia Trinità. J. Vallès, 17/11/2015 (BCN 126585)	Perennial
Artemisia integrifolia Richards. (Anthemideae)	Russia, Chitin oblast, Kyra, A.A. Korobkov MV19, 26/8/2005 (BCN 136548)	Perennial
Artemisia kurramensis Qazilb. (Anthemideae)	Pakistan, Parachinar: Kurram Agency, Federally Administered Tribal Areas. Sh. Bibi, 5/2014 (ISL QAU26860)	Perennial
Artemisia rutifolia Stephan ex Spreng. (Anthemideae)	Russia, Chitin oblast, Khapcharang, A.A. Korobkov MV4, 9/9/2005 (BCN 136546)	Perennial
Artemisia sericea Weber ex Stechm. var. *nitens* (Steven ex Besser) Steven ex Krasch. (Anthemideae)	Russia, Krasnoyarsk. N.V. Stepanov MV26, 14/10/2005 (BCN 136547)	Perennial
Artemisia vallesiaca All. (Anthemideae)	Switzerland, Valais: Sion, pathway to Montorge. J. Vallès & A. Vehí, 24/8/2014 (BCN 114077)	Perennial
Baccharis halimifolia L. (Astereae)	France: Orsay, Université de Paris-Sud XI garden (001100), from eastern North America. S. Siljak-Yakovlev & J. Vallès, 7/1/2016 (BCN 127893)	Perennial
Bidens alba (L.) DC. (Heliantheae)	France, Guadeloupe island, Guadeloupe Basse-Terre, Bouillante. S. Siljak-Yakovlev, 23/5/2014 (BCN 136549)	Annual
Inula ensifolia L. (Inuleae)	Croatia: Biokovo mountain. S. Siljak-Yakovlev, 8/7/2016 (BCN)	Perennial
Psiadia retusa DC. (Astereae)	France, Réunion island, cultivated in the Botanical garden from a wild population. S. Siljak-Yakovlev, 8/3/2012 (BCN)	Perennial
Serratula radiata (Waldst. & Kit.) M.Bieb. (Cardueae)	Croatia: Biokovo mountain. S. Siljak-Yakovlev, 8/7/2016 (BCN)	Perennial
Urospermum picroides (L.) Scop. ex F.W.Schmidt (Cichorieae)	1. Croatia, Dubrovnik, S. Siljak-Yakovlev, 8/6/2013 (BCN-S 2077) 2. Croatia, Makarska (Blato), S. Siljak-Yakovlev, 15/7/2015 (BCN-S 2078)	Annual

not yet available. To establish the status of novelty, we used four comprehensive and updated genome size and chromosome number databases, all of them accessed on January 25, 2017: the Kew plant DNA C-values database (http://data.kew.org/cvalues); FLOWer, a flow cytometry-created plant DNA database (http://botany.natur.cuni.cz/flower/index.php); GSAD, an Asteraceae genome size database (http://www.etnobiofic.cat/gsad); and the Index to chromosome numbers in Asteraceae (http://www.lib.kobe-u.ac.jp/infolib/meta_pub/engG0000003asteraceae).

MATERIALS AND METHODS

Materials. Fresh leaf material of the investigated taxa was collected for genome size measurements from adult plants or from seedlings. For adult plants, it was preserved in slightly humidified tissue paper and kept in a refrigerator until processing on the cytometer, less than one week after collection. For seedlings, the cotyledons were processed directly. Root tips from either plants living in pots or germinated seedlings were used for chromosome counts. In addition, material for herbarium vouchers was collected, pressed, and deposited in one of two herbaria, BCN (*Centre de Documentació de Biodiversitat Vegetal, Universitat de Barcelona*) or ISL (Biological Sciences Department, Quaid-I-Azam University, Islamabad). Data on plant origin and collection are provided in Table 1, together with information about the life cycle type of the studied taxa.

Flow cytometry. Genome size was assessed either at the *Centres Científics i Tecnològics, Universitat de Barcelona* (hereafter Barcelona; *Artemisia*) or at the *Institut des Sciences du Végétal*, CNRS, Gif-sur-Yvette (hereafter Gif; other taxa), using in both cases the following three of five internal standards of the latter institution in order to cover the range of DNA contents: *Solanum lycopersicum* L. 'Montfavet 63-5' (2C = 1.99 pg, Lepers-Andrzejewski *et al.* 2011); and *Petunia hybrida* Vilm. 'PxPc6' and *Pisum sativum* L. 'Long Express' (2C = 2.85 pg and 8.37 pg, respectively, Marie & Brown 1993).

The total nuclear DNA amount was assessed by flow cytometry according to Marie & Brown (1993). Young leaves or cotyledons of the analysed individuals and the internal standards were chopped together using a razor blade in a plastic Petri dish with 1200 µl of LB01 isolation buffer (Doležel *et al.* 1989; Barcelona) or 1 ml of Gif nuclei-isolation buffer, which is slightly modified Galbraith's buffer (Galbraith *et al.* 1983): 45 mM $MgCl_2$, 30 mM sodium citrate, 60 mM MOPS (4-morpholine propane sulphonate, pH 7), and 1% (w/v) polyvinylpyrrolidone 10000, pH 7.2) containing 0.1% (w/v) Triton X–100, supplemented with 5 mM sodium metabisulphite and RNase (2.5 U/ml) (Gif). Barcelona's buffer was also supplemented with 100 µg/ml of ribonuclease A (RNase A, Roche, France). The suspension was filtered through 70 (Barcelona) or 50 (Gif)-µm nylon mesh. The nuclei were stained with 60 (Barcelona) or 50 (Gif) µg/ml propidium iodide, a specific DNA intercalating fluorochrome dye, and kept at least 5 min at 4°C. Between 5000 and 10000 stained nuclei were measured for each sample using either a flow cytometer with a 488-nm 15 mW laser (Epics XL, Beckman Coulter, Brea, CA, USA; Barcelona) or one with a 532-nm 30 mW laser (CyFlow SL3, Partec, Munster, Germany; Gif). The total holoploid nuclear DNA content (2C) was calculated using the linear relationship between the fluorescent signals from stained nuclei of the investigated species and the internal standard. The mean 2C-value as well as the standard deviation of the mean and its coefficient of variation (%) were calculated from measurements of samples comprising two to five individuals (one individual – in two replicates in one case, i.e., that of a second, complementary population of one taxon) according to the samples.

Chromosome number determination. Achenes were germinated on wet filter paper in Petri dishes at room temperature. Young plants were grown in pots in greenhouse conditions. Root tips obtained from the seedlings or from the potted plants were pretreated with 0.05% aqueous colchicine at room temperature for from 1 h 30 min to 2 h 45 min and then fixed in absolute ethanol and glacial acetic acid (3:1) for at least 12 hours at 4°C. Root tips were hydrolysed in 1 M HCl for 1-5 minutes at 60°C, washed in distilled water at room temperature, and stained in 1% orcein in 45% acetic acid for 0.5-12 hours at room temperature. Root tip meristems were squashed in a droplet of 45% acetic acid and glycerol (9:1) and observed in Zeiss Axioplan (Barcelona) or Zeiss Axiophot (Orsay) microscopes, where the best metaphase plates were photographed using an Axiocam HRm camera (Zeiss, Oberkochen, Germany; Barcelona) or a CCD camera (RETIGA 2000R; Princeton Instruments, Evry, France; Orsay).

RESULTS AND DISCUSSION

Data on nuclear DNA content (mean 2C-values per taxon studied) of the 14 populations (12 taxa) studied, including standard deviations and coefficients of variation, are presented in Table 2. The coefficients of variation range from 0.57 to 3.56% (mean value, 1.65), indicating reliable and reproducible estimates, and uniform populations.

According to the sources mentioned in the Materials and Methods section, the obtained values are the first genome size data for all the taxa considered, in most cases at the specific level and in one case, *Artemisia sericea* Weber ex Stechm. var. *nitens* (Steven ex Besser) Steven ex Krasch., at the varietal level. For *Artemisia vallesiaca* All., this is the first determination in a wild population, the results (2C = 9.82 pg) being close to previous reports

Table 2. Nuclear DNA content and chromosome numbers of the taxa studied.

Taxon (tribe)	Number of individuals studied	2C in pg (standard deviation)[1]	Coefficient of variation for this mean (%)	1C in Mbp[2]	Internal standard[3]	Chromosome number ($2n$)[4]
Artemisia densiflora Viv., population 1 (Anthemideae)	5	6.39 (0.08)	2.84	3125	*Pisum*	18^{+}
Artemisia densiflora Viv., population 2 (Anthemideae)	1	6.37 (0.10)	2.75	3115	*Pisum*	18^{+}
Artemisia integrifolia Richards. (Anthemideae)	5	5.22 (0.24)	2.50	2553	*Pisum*	$18, 36^{++}$
Artemisia kurramensis Qazilb. (Anthemideae)	5	5.58 (0.07)	2.50	2729	*Petunia*	18^{++}
Artemisia rutifolia Stephan ex Spreng. (Anthemideae)	5	5.56 (0.13)	0.85	2719	*Petunia*	18^{++}
Artemisia sericea Weber ex Stechm. var. *nitens* (Steven ex Besser) Steven ex Krasch. (Anthemideae)	5	23.68 (0,78)	0.59	11580	*Pisum*	$18, 36, 90^{++,+++}$
Artemisia vallesiaca All. (Anthemideae)	5	9.82 (0.09)*	3.56	4802	*Pisum*	36^{++}
Baccharis halimifolia L. (Astereae)	2	4.41 (0.08)	1.92	2156	*Petunia*	18^{++}
Bidens alba (L.) DC. (Heliantheae)	5	4.19 (0.03)	0.74	2049	*Petunia*	48^{+}
Inula ensifolia L. (Inuleae)	3	3.62 (0.03)	0.73	1770	*Solanum*	$16, 24^{++}$
Psiadia retusa DC. (Astereae)	3	7.68 (0.04)**	0.57	3756	*Petunia*	?
Serratula radiata (Waldst. & Kit.) M.Bieb. (Cardueae)	5	3.67 (0.02)	0.61	1795	*Solanum*	$30, 60^{++}$
Urospermum picroides (L.) Scop. ex F.W.Schmidt (Cichorieae), population 1	5	1.37 (0.02)	1.56	670	*Solanum*	10^{+}
Urospermum picroides (L.) Scop. ex F.W.Schmidt, population 2	5	1.38 (0.01)	0.94	675	*Solanum*	10^{+}

[1]All reports are first estimates; one and two asterisks (*) indicate a genome size report obtained for the first time from wild materials (in a species for which genome size had been previously assessed only from botanical garden materials) and a report new for a genus, respectively.
[2]1 pg = 978 Mbp (Doležel *et al.* 2003).
[3]See the Materials and Methods section for details.
[4]One and two plus signs (+) indicate, respectively, our own counts in this paper and data from K. Watanabe's Index to chromosome numbers in Asteraceae (http://www.lib.kobe-u.ac.jp/infolib/meta_pub/engG0000003asteraceae, accessed January 25, 2017). Three plus signs indicate that the chromosome numbers are provided for the species without varietal identification.

on plants cultivated in a botanical garden (2C = 9.81, 9.13 pg; Garcia *et al.* 2006; Pellicer *et al.* 2010). The nuclear DNA content found in *Artemisia sericea* var. *nitens* (2C = 23.68 pg) is not very different from that previously reported for the species (without subspecies indication; 2C = 23.33, 23.95, and 24.71 pg; Pellicer *et al.* 2010). Finally, the nuclear DNA amount is here estimated for the first time in one genus, *Psiadia* Jacq. ex Willd.

The chromosome number is provided for the first time for *Artemisia densiflora* Viv. This number ($2n$ = 18), indicating a diploid level, coincides with that of *A. caerulescens* L. (Vallès & Seoane 1987), under which this taxon has been combined [*A. caerulescens* subsp. *densiflora* (Viv.) Gamisans ex Kerguélen & Lambinon], although molecular data do not support a close relationship between the two species (Malik *et al.*, 2017). For *Bidens alba* (L.) DC. and *Urospermum picroides* (L.) Scop. ex F.W.Schmidt, numbers of $2n$ = 48 and 10, respectively, have now been confirmed (Queirós 1973; Tereza *et al.* 2006). Metaphase plates of our counts are presented in Fig. 1.

The nuclear DNA amounts here recorded are rather small or medium-sized. According to the categories established by Leitch *et al.* (2005), one out of the 12 (8.3%) genome sizes estimated here falls within the category of very small (2C < 2.8 pg), whereas most of them [eight (66.7%)] are small (2.8 ≤ 2C < 7), three (25%) are intermediate (7 ≤ 2C < 28), and none is large (28 ≤ 2C ≤ 75) or very large (2C > 75). As for the ploidy level, diploids dominate, complemented by the presence of a few polyploids (three tetraploids and one decaploid).

The 2C values here assessed vary from 1.37 to 23.68 pg, values falling within the range of the family, viz., from 0.72 to 142.0 pg (http://www.asteraceaegenomesize.com, updated December 31, 2016, accessed January 25, 2017).

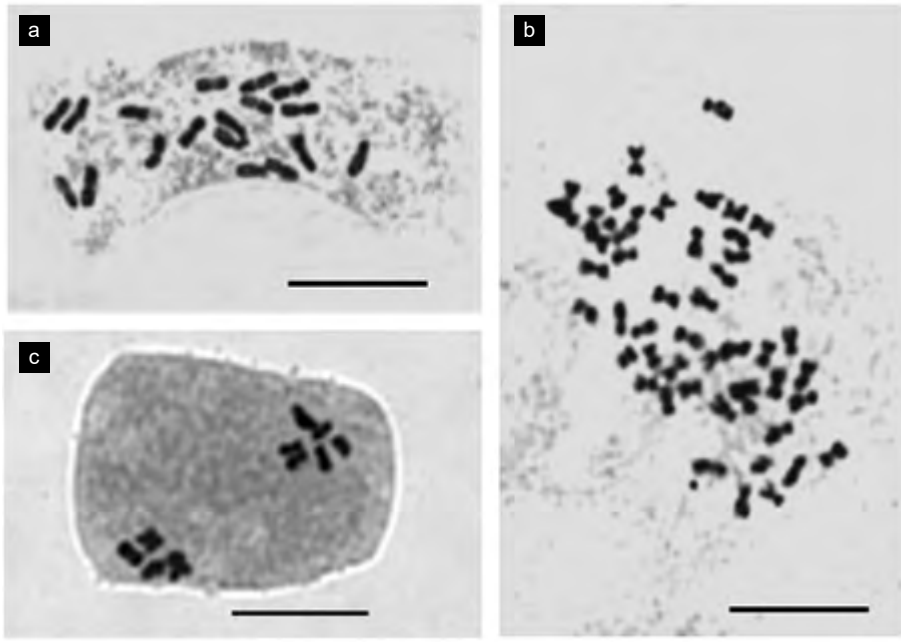

Figure 1. Metaphase plates of *Artemisia densiflora*, population 1, 2n = 18 (A); *Bidens alba*, 2n = 48 (B); and *Urospermum picroides*, population 1, 2n = 10 (C). Scale bars = 10 µm.

At the species level, according to the same database, most of our values also fall within the range of variation known for their respective genera, with two exceptions. The present recorded value for *Baccharis hamilifolia* (2C = 4.41 pg) represents the lowest value to date in the genus, the previous ones ranging from 4.78 to 6.72 pg. *Serratula radiata* (Waldst. & Kit.) M.Bieb. (Cardueae) has a genome size (2C = 3.67 pg) more than double that of the only other species of the genus for which such a parameter is available (*S. pusilla* Dittrich, 2C = 1.50 pg; Bou Dagher-Kharrat *et al.* 2013), which might indicate a higher ploidy level in the genus.

CONCLUDING REMARKS

With just 1% of the 1,200 species that Garcia *et al.* (2014) proposed for study in the period 2014-2018, the present paper adds only a small amount of data to the knowledge of genome size in the family Asteraceae. Moreover, with three out of the 12 taxa (four out of the 14 populations) coming from Croatia (*Inula ensifolia*, *Serratula radiata*, and *Urospermum picroides*), it contributes nuclear DNA content information on plants from the Balkan region, where already ca. 15% of the flora has genome size data available (Vallès *et al.* 2014), thus modestly expanding the Balkan flora genome size database (Siljak-Yakovlev *et al.* 2010). Although the current dataset for genome size and chromosome numbers is numerically minor, we think that any new contribution to knowledge of those fundamental biological parameters should be considered valuable and ought to be encouraged. Such contributions expand existing knowledge in the karyological/cytogenetic field and provide more data suitable for resolving many kinds of systematic and evolutionary issues related to different species or genera, including taxonomic aspects (Stuessy 2011). They are also valuable for meta-analytical work on larger groups, such as families or all angiosperms (Bennett & Leitch 2011; Garcia *et al.* 2014).

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REZIME

Prilog poznavanju količine jedarne DNK u familiji Asteraceae: prve procene za jedan rod i 12 vrsta, sa brojem hromozoma za tri vrste

Joan Vallès, Sadia Malik, Mario Gomez i Sonja Siljak-Yakovlev

U ovom radu su predstavljene prve procene, tečnom citometrijom, količine jedarne DNK za jedan rod, 11 vrsta i 1 varijetet (uključujući prve podatke za material iz prirode jedne od vrsta), svih iz familije Asteraceae. Broj hromozoma je prikazan za tri vrste, uklučujući nove podatke za jednu vrstu. Ovi podaci dopunjuju postojeće informacije o veličini genoma u najvećoj familiji biljaka.

Ključne reči: 2C-vrednost, Asteraceae, Compositae, tečna citometrija, količina jedarne DNK, vaskularne biljke.