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Genome size in wild and cultivated peanut germplasm

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Summary. Genome size of 16 species of *Arachis* L. with $x = 10$ and three with $x = 9$ was determined. DNA content (2C) between all diploid species, varies from 2.87 pg in *A. retusa* to 6.59 pg in *A. douradiana*. Considering species with $2n = 2x = 20$ of all the sections, it suggests that in the evolution of *Arachis* genome, both increases and diminutions of DNA content would have occurred. Species with greater DNA content are included in sections believed to have a more recent origin, whereas those that contain minor DNA belong to the oldest sections; therefore, we propose genome evolution of *Arachis* toward higher DNA content. Origin of the basic chromosome number $x = 9$ is discussed considering genome size variation between species with $x = 10$ and $x = 9$. Reduction of the DNA content after the polyploidization would have happened in *A. hypogaea.*

Keywords: *Arachis*; peanut; DNA content; genome evolution; phylogenetic relationships; aneuploidy

Arachis is an exclusively South American genus and presents around eighty annual or perennial species (Krapovickas and Gregory 1994; Valls and Simpson 2005). They are organized in nine sections (*Trierectoides*, *Erectoides*, *Extranervosae*, *Triseminatae*, *Heteranthae*, *Caulorrhizae*, *Procumbentes*, *Rhizomatosae* and *Arachis*), according to morphology, chromosomal characteristics, and relations of cross-compatibility.

Two basic chromosome numbers are known for the genus, $x = 10$, with diploid and tetraploid taxa, and $x = 9$ only found in diploids. The basic number $x = 10$ is present in all sections and in most of the species, whereas $x = 9$, has been so far found in only four species, *A. palustris* (Lavia 1996), *A. praecox* (Lavia 1998) and *A. decora* (Peñaloza et al. 1996) of section *Arachis*, and *A. porphyrocalyx* of section *Erectoides* (Peñaloza and Valls 2005). It has been suggested that the $x = 9$ constitutes a derived number from $x = 10$ (Lavia 1998), but the cytogenetic mechanism involved in its origin is not yet known with certainty.

Taxonomic and crossing compatibility studies suggested that *Trierectoides*, *Erectoides*, *Extranervosae*, *Triseminatae* and *Heteranthae* are the oldest sections while *Procumbentes*, *Caulorrhizae*, *Rhizomatosae* and *Arachis* are of more recent origin (Krapovickas and Gregory 1994). Considering karyotype symmetry, Fernández and Krapovickas (1994) and Lavia (1999, 2001) have proposed that the *Trierectoides* is the most primitive section of the genus, whereas the *Arachis* section would be one of the most recent origin. However, phylogenetic relationships

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between the sections of the genus are still not fully understood.

The study of DNA content has contributed with valuable data to infer evolutionary trends within particular plant groups analyzing subjects such as origin of different basic chromosome number (Martel et al. 1997), changes of karyotype symmetry (Martínez and Ginzo 1985; Poggio et al. 1986; Brandham and Doherty 1998) and changes of karyotype length (Martínez and Ginzo 1985). Even though some reports on DNA content have been done in the genus *Arachis* (Resslar et al. 1981; Singh et al. 1996), they included one third of the species so far known and neither relationships have been established between changes in DNA content and karyotype structure nor with the origin of different basic chromosome number.

In this context, we have determined the nuclear DNA content of sixteen species with $x = 10$ and three with $x = 9$, with the following objectives: (1) to analyze the relationships between of DNA content variation and changes of karyotype symmetry, (2) to determine the DNA content of species with different basic numbers in order to bring light on the origin of $x = 9$, and (3) to analyze the DNA content between species and sections to contribute in the understanding of the phylogenetic relationships of the genus.

Materials and methods

The analyzed material is presented in Table 1. The seeds were obtained from INTA Manfredi (Córdoba, Argentina), CENARGEN-EMBRAPA (Brasilia, Brazil) and Texas Agricultural Experiment Station (Stephenville, USA). Voucher specimens have been deposited in the herbarium of the Instituto de Botánica del Nordeste (CTES).

The nuclear DNA content was measured in secondary root-tips according to Feulgen method and computer-based image cytometry (Vilhar et al. 2001). *Allium cepa* "Alice" was used as standard (2C = 30.84 pg) (Vilhar et al. 2001). Roots of *Arachis* species and *A. cepa* were fixed in ethanol:acetic acid (3:1) for 24 h at 4°C. The material was hydrolyzed in 5 N HCl by 1 h at 22°C and stained with Schiff reagent. Slides were observed in a Zeiss Axioskop microscope, the images captured with CCD digital camera and analyzed with Global software Lab Image, SPO 550, version 3.1 (Microsoft Windows). Three plants of each species and three roots per plant were analyzed. Each slide was prepared placing one root tip of the target species one of the standard aside of it. The integrated optical density (IOD) was measured in ten nuclei per root tip. The mean and the standard error were determined per root tip and averaged for each species. The 2C value was calculated according to the formula:

$$[\text{IOD } \textit{Arachis} \times \text{nuclear DNA content of } \textit{A.cepa} \; (30.84\text{pg})]/\text{IOD } \textit{A. cepa}$$

Results

DNA content estimations are detailed in Table 1. Chromosomal characteristics previously reported are also included in the same table.

DNA content (2C) between all diploid species of *Arachis*, varies from 2.87 pg in *A. retusa* to 6.59 pg in *A. douradiana* (Table 1). The species with greater DNA content have correspondingly the longest chromosomes while those with lower contents have smallest chromosomes (Fig. 1). Therefore, increases and decreases of the DNA content are directly related with the chromosome size in the genus *Arachis*.

Among all, section *Arachis* needs particular attention because it has two different basic numbers, $x = 9$ and $x = 10$ and two ploidy levels, $2x$ and $4x$. Considering the chromosome numbers, the species studied here can be divided into three groups: (1) species with $2n = 2x = 18$: *A. palustris*, *A. decora* and *A. praecox*; in which the DNA 2C value varied from 3.26 pg in the former to 4.16 pg in *A. decora*, having the smallest and the longest chromosome length, respectively. *Arachis praecox* showed intermediate values both in DNA content and total chromosome length. All these species has the same karyotype formula, 16m + 2sm. (2) Species with $2n = 2x = 20$: *A. batizocoi*, *A. herzogii*, *A. stenosperma* and *A. chiquitana*. *Arachis herzogii* is the species with lowest DNA content and smallest chromosome length of the group (2.04 μm), whereas *A. stenosperma* presents the greatest DNA content and the

Table 1. Species, collectors and procedence, chromosome number ($2n$), DNA amounts expressed in picograms (pg) for holoploid genome (2C) and monoploid genome size (Cx) (Greilhuber et al. 2005). Chromosome length by monoploid genome (CL) in micras, centromeric index (CI) and karyotype formula (K). The abbreviations used in the karyotype formula refer to chromosome types: m metacentric, sm submetacentric

Species	Collectors and procedence	$2n$	2C ± SE	Cx	Chromosomal features		
					CL	CI	K
Section							
Erectoides							
A. douradiana Krapov. & W. C. Gregory	VMPzW 14067. Brasil, MS, Mun. Dourados, 22°14'S, 54°58'W.	20	6.59 ± 0.20	3.29	29.6[c]	43.96[c]	18m + 2sm[c]
Section							
Extranervosae							
A. macedoi Krapov. & W. C. Gregory	VR 7533. Brasil, MG, Capinopolis, Faz. Santa Terezinha.	20	3.17 ± 0.08	1.58	15.2[e]	44.35[e]	20m[e]
A. retusa Krapov. & W. C. Gregory	VPmSv 12939. Brasil, TO, Mun. Paranã, Paranã, 12°37′ S 47°53′ W.	20	2.87 ± 0.12	1.43	14.1[e]	40.76[e]	14m + 6sm[e]
A. burchellii Krapov. & W. C. Gregory	VKRSv 6556. Brasil, TO, Mun. Colinas do Tocantins, 3 km S de Araguaina, BR-153.	20	3.27 ± 0.17	1.63	–	–	–
A. pietrarellii Krapov. & W. C. Gregory	VK 12085. Brasil, MT, Mun. Nobres: 900 m ao N do Corrego Seco.	20	2.99 ± 0.06	1.49	–	–	–
A. villosulicarpa Hoehne	VKSSv 8820. Brasil, MT, Aldeia Aroeira (cerca de Vilhena).	20	3.18 ± 0.15	1.59	–	–	–
Section							
Trisemintae							
A. triseminata Krapov. & W. C. Gregory	VFaPzSv 13080. Brasil, MG, Mun. Janaúba, 15°2′́S, 43°2′́W.	20	2.96 ± 0.07	1.48	–	–	–
Section							
Heteranthae							
A. giacomettii Krapov., W. C. Gregory, Valls & C.E. Simpson	WPn 201. Brasil, MG, 8,5 km NW de Montalvania, na estrada para Pitarana.	20	3.98 ± 0.17	1.99	–	–	
A. sylvestris (A. Chev.) A. Chev.	VVeSv 8520. Brasil, PI, Mun. Oeiras, 35 km NE de Cristino Castro, BR-135.	20	3.00 ± 0.12	1.50	15.3[e]	42.37[e]	16m + 4sm[e]
Section							
Procumbentes							
A. appressipila Krapov. & W. C. Gregory	VPoBi 9077. Brasil, MS, Faz. Coqueiro, 17 km desde a BR-262 pela estrada para Forte Coimbra.	20	5.66 ± 0.18	2.83	23.8[c]	42.73[c]	14m + 6sm[c]
A. vallsii Krapov. & W. C. Gregory	VRGeSv 7635. Brasil, MS, 37,8 km a oeste da saida de Miranda na BR-262.	20	5.86 ± 0.18	2.88	17.7[c]	44.61[c]	18m + 2sm[c]

Table 1. (Continued)

Species	Collectors and procedence	2*n*	2C ± SE	Cx	Chromosomal features		
					CL	CI	K
Section							
Arachis							
A. batizocoi Krapov. & W. C. Gregory	K 9505. Bolivia, Santa Cruz, Cordillera, Parapetí.	20	4.97 ± 0.21	2.48		39.14[a]	12m + 6sm + 2st[a]
A. herzogii Krapov., W. C. Gregory & C.E. Simpson	KSSc 36030. Bolivia, Santa Cruz, Prov. Chiquitos, 60°47′W, 17°47′S.	20	4.21 ± 0.16	2.10	20.4[e]	43.79[e]	18m + 2sm[e]
A. chiquitana Krapov., W. C. Gregory & C.E. Simpson	KSSc 36027. Bolivia, Santa Cruz, Prov. Chiquitos, 60°47′W, 17°47′S.	20	5.10 ± 0.22	2.55	20.6[e]	44.25[e]	18m + 2sm[e]
A. stenosperma Krapov. & W. C. Gregory	VKSSv 9010. Brasil, MT, 32 Km E de Cuiabá, BR-364.	20	5.74 ± 0.20	2.87	–	–	18m + 2sm[e]
	VGaSv 12646. Brasil, MT, Santo Antonio do Leverger 15°43′S, 55° 42′W.	20	5.62 ± 0.14	2.81	–	–	18m + 2sm[e]
A. praecox Krapov., W. C. Gregory & Valls	VSGr 6416. Brasil, MT, Mun. Barra do Bugres, 71 km N de Cáceres.	18	3.61 ± 0.05	1.80	17.64[b]	43.47[b]	16m + 2sm[b]
A. palustris Krapov., W. C. Gregory & Valls	VPmSv 13023. Brasil, TO, Mun. Filadelfia, 7°25′S, 43°37′W.	18	3.26 ± 0.09	1.63	16.65[b]	43.64[b]	16m + 2sm[b]
A. decora Krapov., W. C. Gregory & Valls	VSW 9955. Brasil, GO, Mun. Campos Belos, 13°01′S 46°42′W.	18	4.16 ± 0.09	2.08	16.83[e]	45.41[e]	16m + 2sm[e]
A. hypogaea L.							
ssp. *hypogaea* var. *hypogaea*	RCM 1457, Sopachuy, BOL	40	10.87 ± 0.31	2.71	18.2[d]	45.81[d]	38m + 2sm[d]
ssp. *fastigiata* var. *fastigiata*	US 684, Rosita, ECU	40	10.92 ± 0.12	2.73	19.7[d]	45.18[d]	38m + 2sm[d]
ssp. *fastigiata* var. *equatoriana*	US 714, Zaruma, ECU	40	11.08 ± 0.32	2.77	18.1[d]	45.75[d]	38m + 2sm[d]

Collectors: Bi = L. B. Bianchetti, Fa = Faraco de Freitas, Ga = M. L. Galgaro, Ge = M. A. N. Gerin, Gr = A. Gripp, K = A. Krapovickas, M = J. P. Moss, Pm = R. N. Pittman, Pn = P. Pinheiro, Po = A. Pott, Pz = E. A. Pizarro, R = V.R. Rao, Ro = D. M. S. Rocha, S = C. E. Simpson, Sa = H. T. Stalker, Sc = A. Schinini, Sv = G. P. Silva, V = J. F. M. Valls, Ve = R. F. de ArrudaVeiga, W = W. L. Werneck, Wi = D. E. Williams

[a] Fernández and Krapovickas (1994); [b] Lavia (1998); [c] Lavia (2001); [d] Lavia and Fernández (2004); [e] Lavia (unpublished)

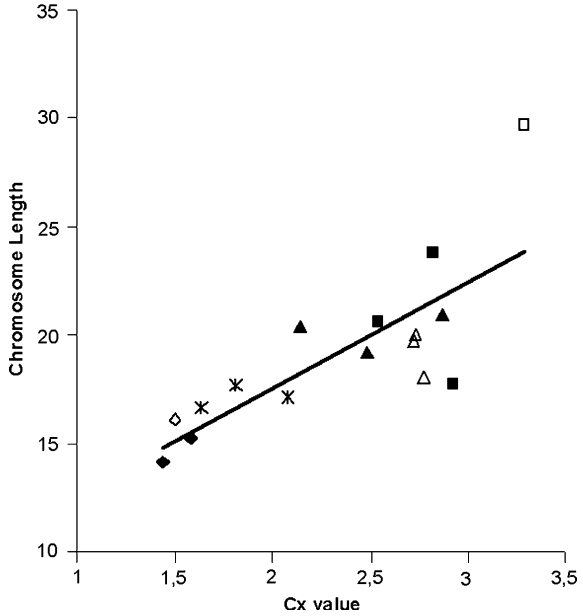

Fig. 1. Relationship between content of DNA (Cx value) and chromosome length by monoploid genome in different sections of *Arachis*. *Open triangle* Arachis $2n = 40$, *filled triangle* Arachis $2n = 20$, *Asterisk* Arachis $2n = 18$, *open square* Erectoides, *filled square* Procumbentes, *open diamond* Heteranthae, *filled diamond* Extranervosae

longest chromosomes. Considering the karyotype formula, *A. herzogii*, *A. chiquitana* and *A. stenosperma* display 18m + 2sm, whereas *A. batizocoi* has a more asymmetric karyotype, with 12m + 6sm + 2st. (3) Species with $2n = 4x = 40$: *A. hypogaea.* Three botanical varieties of the cultigen were analyzed, two of subsp. *fastigiata* and one of subsp. *hypogaea*. The DNA content varied from 10.87 pg in var. *hypogaea* to 11.08 pg in var. *aequatoriana*. The karyotype of the three varieties is 38m + 2sm.

Considering the other sections, all the studied species have $2n = 2x = 20$. Within section *Erectoides*, *A. douradiana* presents 6.59 pg, with a chromosome length of 2.96 μm and a karyotype formula with 18m + 2sm. The five species analyzed within section *Extranervosae* showed an average of 3.09 pg, varying from 2.87 pg in *A. retusa* to 3.27 pg in *A. burchellii.* The former is the only species of the section for which karyotype data are known, having 1.41 μm of chromosome length and karyotype formula of 14m + 6sm. *Arachis triseminata* belongs to the monotypical section *Triseminatae*, and presents 2.96 pg of nuclear DNA content. DNA content within section *Heteranthae* oscillates between 3 pg in *A. sylvestris* and 3.98 pg in *A. Giacomettii*. *Arachis sylvestris* has a karyotype formula of 16m + 4sm and 1.53 μm of mean chromosome length. Finally, *A. appressipila* and *A. vallsii* of section *Procumbentes* have 5.66 and 5.86 pg, respectively, with a karyotype formula of

Table 2. DNA values (2C) previously reported and data aported in the present work

Species	2C value (pg)			
	Resslar et al. (1981)	Singh et al. (1996)	Temsch and Greilhuber (2000)	Present work
A. appressipila		6.02		5.66
A. batizocoi	4.96	5.33		4.97
A. stenosperma	5.53	5.82		5.68[a]
A. sylvestris		3.02		3.00
A. triseminata		3.04		2.96
A. villosulicarpa		3.76		3.18
A. hypogaea subsp. *hypogaea* var. *hypogaea*	10.36	11.31[a]	5.931[a]	10.87
A. hypogaea subsp. *fastigiata* var. *fastigiata*	11.10	10.93[a]	5.946	10.92

[a] Mean values

14m + 6sm and 2.38 μm of mean chromosome length in the former and 18m + 2sm and 1.77 μm in the latter.

Discussion

Estimations of DNA content were made in 18 wild species and three botanical varieties of the cultigen *A. hypogaea*. Our results extends the knowledge of DNA content to 50% of the species of *Arachis* and is the first to include species with basic number $x = 9$.

Variations in the nuclear DNA content can occur in all the taxonomic categories, even between very closely related species (Jackson 1971; Price 1988). Considering all the sections analyzed and comparing only the diploid species with $x = 10$ DNA content differs 2.29 times (3.72 pg) among the species, in spite of the constancy of chromosome number. The great variation existing in DNA values between and within families and genus is not always correlated with structural or evolutionary complexity, and it is known as the C value paradox (Thomas 1971).

Previous data of DNA content (Resslar et al. 1981; Singh et al. 1996; Temsch and Greilhuber 2000) for some of the species studied here are shown in Table 2. Comparing the data, our results confirm the DNA values of *A. stenosperma*, *A. sylvestris* and *A. triseminata* found by Singh et al. (1996), and those published by Resslar et al. (1981) for *A. batizocoi* and *A. stenosperma*. Nevertheless, our values for *A. appressipila*, *A. batizocoi* and *A. villosulicarpa* are different from those published by Singh et al. (1996). On the other hand, the data obtained by us for *A. hypogaea* varieties agrees with those of Resslar et al. (1981) and Singh et al. (1996), but not with that published by Temsch and Greilhuber (2000). However, the scarce intraspecific variation we found for three varieties of *A. hypogaea* is coincident with the results obtained by Temsch and Greilhuber (2000).

Differences in DNA content reported by different authors for same species could be explained by the use of different fixations, since Singh et al. (1996) used double fixation in 4% formaldehyde and ethanol:acetic acid (3:1), Temsch and Greilhuber (2000) used 4% formaldehyde and extensive rinses with methanol:acetic acid (3:1) whereas Resslar et al. (1981) and in the present work ethanol:acetic acid (3:1) was used. Another cause that could explain the differences in DNA values would be the analysis of different accessions, for example in *A. stenosperma*, Resslar et al. (1981) studied HLK 408, HLK 409 and HLK 410 collections, whereas we analyzed the VKSSv 9010 and VGaSv 12646. In the case of *A. appressipila*, *A. batizocoi* and *A. villosulicarpa* we cannot attribute the discrepancies to different accessions since Singh et al. (1996) did not include this information.

Content of DNA and evolution of karyotype

One of the chromosomal parameters used to establish tendencies in the evolution of karyotype is the chromosomal symmetry. The generally accepted statement that symmetrical karyotypes are more primitive than asymmetrical ones (Stebbins 1971) is frequently cited between the cytogenetists. On the other hand, changes of karyotype symmetry have been related to the increases or the diminutions of the DNA content. It has been stated that chromosomal complements with higher DNA content tend to be more symmetrical than those with lower content (Rees 1984). In *Oxalis*, however, higher DNA content was observed in species with more asymmetrical karyotypes (Martínez and Ginzo 1985). In other cases, both increases and diminutions of the DNA content have accompanied increases of karyotype asymmetry (Poggio et al. 1986), while in *Aloe*, increases of the DNA content did not change the symmetry of the karyotypes (Brandham and Doherty 1998).

Considering diploids with $2n = 2x = 20$ of all the sections, species with symmetrical karyotypes (20m, 18m + 2sm), as well as those with most asymmetrical karyotypes (16m + 4sm, 14m + 6sm, 12m + 6sm + 2st), present low and high DNA contents independently. This fact suggests that in the evolution of the *Arachis* genome, both increases and diminutions of DNA content would have occurred, leading to symmetric or asymmetric karyotypes. Therefore, the gains and losses of DNA content would have

produced amplifications or deletions respectively and of small segments distributed unequally in the chromosomal complement.

On the other hand, even though the species with $x = 9$ have differences in the DNA content (Table 1), they share the same karyotype formula (Lavia 1998, 1999), suggesting proportional increases and reductions in the chromosome arms leading to the maintenance of karyotype symmetry.

Origin of the basic number $x = 9$

The mechanisms responsible for the diminution of chromosome number can be aneuploidy or disploidy (Greilhuber and Ehrendorfer 1988). Aneuploidy implies diminution of the number of chromosomes with loss of DNA content; while disploidy reduces the chromosomal number by means of chromosomal rearrangement without causing considerable variations in the DNA amount.

It has been suggested that the *Arachis* species with $2n = 2x = 18$ would have originated from a diploid species with $x = 10$ ($2n = 2x = 20$), belonging to A or B genome (Lavia 1998; Tallury et al. 2005) as a consequence of aneuploid reduction (Lavia 1996, 1998).

The fact that 18 chromosomes can be arranged in 9 pairs (Lavia 1998, 1999), and that in meiosis form 9 II (Lavia et al., unpublished) it would suggest that the species with $x = 9$ have lost a pair of homologous chromosomes, corresponding to a nulisomic state ($2n = 18$). The chromosomal reduction would have occurred as a result of the union of gametes $n - 1$ chromosomes ($n = 9$). Our results showed that the average DNA content (2C) of the diploid species with basic number $x = 10$ belonging to the Arachis section is 5.13 pg, whereas the average of those with $x = 9$ is 3.67 pg. Since there is a DNA content decrease in the $x = 9$ species, a first approach would indicate that aneuploidy have been the mechanism involved in basic chromosome change. However, the difference of average DNA content between the species with $x = 9$ and $x = 10$ (1.46 pg) are greater to that expected for a unique chromosome pair (calculated dividing the number of chromosomes by the mean 2C value of species with $x = 10$). This fact implies that, if aneuploidy is the mechanism involved in chromosome change, it must have been accompanied by additional DNA losses in the whole complement.

Nevertheless, disploidy as a mechanism of chromosome number change in *Arachis* cannot be ruled out.

Phylogenetic relationships

The nuclear DNA content has an important function in the evolution and adaptation of the plants (Bennett 1982; Price 1976, 1988), therefore DNA content comparison between different taxons may contribute to clarify phylogenetic relationships and to establish evolutionary trends. Our results indicate that the species within sections *Extranervosae*, *Heteranthae* and *Triseminatae* have the lowest values of DNA content, and that the entities of the sections *Arachis*, *Erectoides* and *Procumbentes* show the highest ones (Fig. 2). So far, there is no available information about the DNA content of Trierectoides species, but the chromosomal studies (Fernández and Krapovickas 1994; Lavia 1998, 1999, 2001) together with

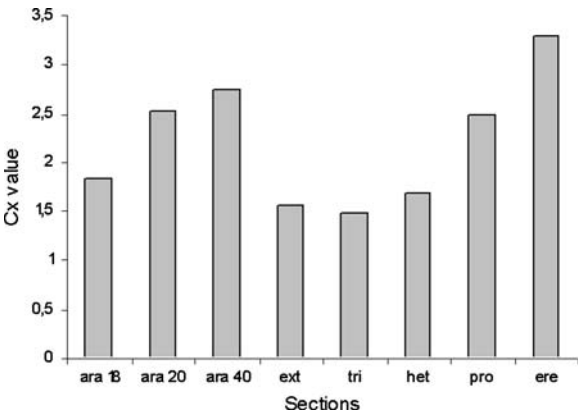

Fig. 2. DNA content average (Cx value) by section. ara 18 = species of section Arachis with 2n = 18, ara 20 = species of section Arachis with 2n = 20, ara 40 = species of section Arachis with 2n = 40, ext = Extranervosae, tri = Triseminatae, het = Heteranthae, pro = Procumbentes, ere = Erectoides

exomorphologic data (Krapovickas 1973), suggest that they would be the most primitive of the genus. With respect to the remaining sections, DNA content is cited in the literature for *A. pintoi* (5.93 pg) of Caulorrhizae section and for a tetraploid *A. glabrata* (11.63 pg) of section *Rhizomatosae* (Singh et al. 1996). Our data on DNA content showed that species with greater DNA content are included in sections believed to have a more recent origin (*Procumbentes*, *Caulorrhizae*, *Rhizomatosae* and *Arachis*), whereas those that contain less DNA belongs to the oldest sections (*Trierectoides*, *Extranervosae*, *Triseminatae* and *Heteranthae*). This tendency towards an increase of DNA content may be explained due to the combined effect of accumulation of retroelements and polyploidy as suggested by Bennetzen and Kellogg (1997) in grasses.

Among the species of section *Arachis* a great DNA content variation is observed (Fig. 2), in part due to the presence of species with different basic numbers and levels of ploidy. The entities with $2n = 18$ present the lowest DNA content, and they are annuals. The presence of characteristics considered derived, such as derived basic number, annuity, precocity, associated with low DNA content, would suggest that the reduction of the DNA content that occurred within this section would have been a recent event and would constitute a secondary tendency in the evolution of the *Arachis* genome.

Although the evolution of the genome of *Arachis* is generally from low values to higher, as it is the general tendency in angiosperms (Leitch et al. 1998; Soltis et al. 2003), the data obtained within the Arachis section support the concept of dynamism in the evolution the genome, involving expansions and retractions, that would have occurred in several opportunities within the Arachis section.

Polyploidy and DNA content

Polyploidy is a frequent event in the angiosperms and relevant in plant evolution (Lewis 1980). It should be expected that the DNA content increases in proportion to the ploidy levels and that the DNA of an amphiploid is equal to the sum of the DNA of its ancestors. Nevertheless, in most amphiploids, the DNA content is reduced by monoploid genome with respect to the ancestors, like in Brassica (Narayan 1998). *Arachis hypogaea* ($2n = 4x = 40$) is an amphiploid, whose most probable diploid ancestors are *A. duranensis* and *A. ipaensis* (Kochert et al. 1991; Fernández and Krapovickas 1994; Seijo et al. 2004). The DNA content of the progenitor species is 5.64 pg in *A. duranensis* and 5.66 pg in *A. ipaensis* (Singh et al. 1996), therefore, the expected value for the cultigen would be 11.30 pg. According to Singh's results the average DNA content of *A. hypogaea* is 11.12 pg, slightly smaller to the expected one. Although this difference is small, this reduction cannot be ignored. DNA reduction in polyploids could be due a rapid non-random elimination of certain non-coding DNA sequences (Liu et al. 1998). In addition, it has been suggested that following polyploidy, an extensive methylation and other mechanism of gene silencing are activated, in part, to repress the spread of transposable elements (Matzke and Matzke 1998). These methylated sequences could become target sequences to be eliminated, providing an additional way to remove excess of DNA in polyploid genomes (Bennett 2000).

From a caryological point of view, the progenitors of *A. hypogaea*, *A. duranensis* and *A. ipaensis*, show the same karyotype formula, 18m + 2sm, (Fernández and Krapovickas 1994), while in the cultigen the formula is 38m + 2sm or 36m + 4sm (Fernández and Krapovickas 1994; Lavia and Fernández 2004; Seijo et al. 2004). These observations show that in spite of the reduction of the DNA content, the karyotype remain symmetrical, therefore the DNA diminution in *A. hypogaea* would have been proportional in the arms of the complement.

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