

Chromosome numbers and ploidy levels of *Paspalum* species from subtropical South America (Poaceae)

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Abstract Somatic chromosome numbers of 131 accessions belonging to 55 *Paspalum* species from subtropical South America have been determined. All species had $x = 10$ as a basic chromosome number, except *P. almum* which had $x = 6$. Six ploidy levels were found among species with tetraploidy as the most frequent condition. New diploid and octoploid counts were reported. For *Paspalum lilloi* and *P. glabrinode* (both $2n = 2x = 20$), and for *P. ellipticum*, *P. erianthoides*, *P. ovale* and *P. remotum* (all $2n = 8x = 80$) sporophytic chromosome numbers are presented for the first time. Records that differ

from previously reported counts are given for the following species: *P. paucifolium* ($2n = 2x = 20$), *P. ceresia* ($2n = 6x = 60$), *P. conjugatum* ($2n = 6x = 60$), *P. alcalinum* ($2n = 6x = 60$) and *P. aff. arundinellum* ($2n + 1 = 5x + 1 = 51$). These chromosome data are discussed in light of ploidy-level variation and implications for breeding systems within and among species.

Keywords Chromosome races · Genetic resources · Grasses · *Paspalum* · Polyploidy

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Introduction

The genus *Paspalum* L. includes about 330–400 species predominantly from the New World (Chase 1929; Zuloaga and Morrone 2005). Species can be found in habitats as diverse as subtropical rainforest, savannas, marshes and dunes, but more frequently are found in the natural grasslands from eastern Bolivia, Paraguay, central and southern Brazil, northern Argentina and Uruguay (Zuloaga and Morrone 2005). Several species are valuable forage or turf grasses cultivated in different parts of the world, e.g. *P. notatum* Flüggé, *P. dilatatum* Poir., *P. atratum* Swallen, and *P. vaginatum* Sw. (Burson and Bennett 1972; Kretschmer et al. 1994; Duncan and Carrow 2000), and their improvement programs are based on the availability of natural variability. Many *Paspalum*

taxa are polyploid and apomictic, which complicates the improvement of breeding stocks through hybridization. In support of breeding programs, we have undertaken a cytogenetic characterization of *Paspalum* accessions, including chromosome counts.

Cytologically, the genus *Paspalum* is complex. Chromosome numbers are known for nearly half the species (Honfi 2003). The basic chromosome number is generally $x = 10$, with a few exceptions (Honfi et al. 1990; Quarin 1992; Norrmann et al. 1994a; Pozzobon et al. 2000; Peñaloza et al. 2008). Polyploidy is a very common feature present in about 80% of the species, with levels varying from $3x$ to $16x$ and tetraploidy the most frequent condition. Apomixis among *Paspalum* species is closely related to polyploidy, but all diploids reproduce sexually. Those species with different chromosome races usually include sexual, out-breeding diploid and apomictic, polyploid cytotypes (Quarin 1992). Both apomixis and polyploidy are important mechanisms influencing the evolutionary biology of *Paspalum* (Burson and Bennett 1970, 1972; Quarin and Hanna 1980; Quarin and Lombardo 1986; Quarin and Norrmann 1987a; Quarin 1992; Burson 1997; Pupilli et al. 1997; Honfi 2003; Daurelio et al. 2004).

A comprehensive collection of *Paspalum* species is needed for various purposes. One is to conserve genetic variability for basic studies and improvement projects. Diploids are the main source of genetic variability and sexual recombination in *Paspalum*; however, their frequency is generally lower than their respective conspecific tetraploids, e.g. $2x$ populations of *Paspalum notatum* inhabit a restricted geographical area in South America, whereas tetraploids are widespread (Burton 1967; Daurelio et al. 2004). In contrast, *Paspalum* polyploids often present fixed genotypes but collectively are adapted to a wide range of ecological conditions, constituting a valuable reserve.

Efforts to obtain chromosome counts of new accessions of *Paspalum* are justified because new chromosome races continue to be discovered (Honfi et al. 1990; Norrmann et al. 1994a; Pozzobon et al. 2000, 2008; Pozzobon and Valls 2003; Morrone et al. 2006; Peñaloza et al. 2008), and because they also provide information about (i) ploidy level, (ii) preliminary assumptions about modes of reproduction, and (iii) the geographic distribution of chromosome races. The objective of this work is to

provide a first step of cytogenetic characterization of *Paspalum* accessions from subtropical South America, based on chromosome numbers and ploidy levels. This contribution is complementary to ongoing phylogenetic studies (Rua et al. 2007; Scataglini et al. 2007). Also, some of the present species are currently included in programmes of comprehensive researches about genetic systems in *Paspalum*, that includes karyology, mode of reproduction, seed-set production and progeny tests (Hojsgaard et al. 2003; Sader and Honfi 2007; Hojsgaard et al. 2008).

Materials and methods

The 55 *Paspalum* species that we studied were collected in five South American countries and identified to species based on classic older and newer taxonomic revisions on the genus (Oliveira and Valls 2002; Oliveira 2004; Zuloaga and Morrone 2005 and references therein), herbarium comparisons and field experience observations.

Cuttings or pieces of rhizomes were obtained in the field and then cultivated in pots at the Universidad Nacional de Misiones, Posadas, Argentina, and at the 'Lucien Hauman' Botanical Garden of the Universidad de Buenos Aires, Buenos Aires, Argentina. These 131 collections originated in eight Argentine Provinces, eight Paraguayan Departments, three Bolivian Departments, and two Brazilian States. All provenances are identified by its herbarium collection number (voucher and collectors). Herbaria are cited following Holmgren and Holmgren (1998). Only part of these collections remain cultivated at Universidad Nacional de Misiones or Lucien Hauman Botanical Garden, some seed samples are preserved at 4°C , and other were not conserved for space reasons (Table 1). Species, localities, vouchers, and herbaria where vouchers have been deposited are detailed in Table 1.

Mitotic studies were performed by examining cut root tips in active growth from cultivated plants when they had 3–4-cm long and then, they were pre-treated with a saturated aqueous solution of 1-bromonaphthalene for 3 h at room temperature. Selected root tips were fixed for 12–24 h in three absolute ethanol: one glacial acetic acid and then conserved in ethanol 70% at 4°C . Most of the pre-treated materials were directly hydrolysed with 1 N HCL at 60°C for 10 min and stained with basic fuchsin. Meristem cells were

Table 1 *Paspalum* species: somatic chromosome number ($2n$), ploidy level (x), locality of origin, vouchers and herbaria where the vouchers are deposited

Species	$2n$	x	Locality and vouchers
<i>Paspalum alcalinum</i> Mez	60**	6x	P. Pdte. Hayes, entre M. Roque Alonso y Clorinda. Rua 303 (BAA, L, MNES) # BAA 22992
<i>P. alnum</i> Chase	12	2x	A. Corrientes, Itá Ibaté. Hojsgaard 330 (MNES, CTES)
	24	4x	A. Misiones, Capital, Posadas. Hojsgaard 189a (MNES, CTES) #
	24	4x	A. Misiones, G. San Martín, Jardín América. Hojsgaard 237 (MNES, CTES)
	24	4x	A. Misiones, Eldorado, Aeroclub. Hojsgaard 240 (MNES, CTES)
<i>P. arundinellum</i> Mez	40	4x	P. Caaguazú, 15 km W de Cnel. Oviedo. Rua 20 (BAA) # BAA 22634
<i>P. aff. arundinellum</i> Mez	50	5x	A. Misiones, Capital, Nemesio Parma. Hojsgaard 270 (MNES, CTES) #
	50	5x	A. Misiones, Capital, Posadas. Hojsgaard 241a (MNES) #
	51**	5x + 1	A. Misiones, Candelaria, Santa Ana. Hojsgaard 224 (MNES)
<i>P. bertonii</i> Hack.	20	2x	A. Misiones, San Ignacio, Club Náutico. Rua 480 (BAA, MNES)
	20	2x	A. Misiones, G. San Martín, Salto Tabay. Rua 482 (BAA, MNES) # BAA 24345
<i>P. ceresia</i> (Kuntze) Chase	60**	6x	B. Santa Cruz, Valle Grande. Rua 327 (BAA, CTES, MNES) # BAA 23216
<i>P. commune</i> Lillo	40	4x	A. Jujuy, P. N. Calilegua, Ruta Prov. 83, El Mirador. Solís Neffa 681 (BAA, CTES, MNES, SI, US)
<i>P. compressifolium</i> Swallen	20	2x	A. Misiones, Capital, Posadas. Hojsgaard 188 (MNES)
<i>P. conjugatum</i> P. J. Bergius	40	4x	A. Jujuy, Ledesma, P. N. Calilegua. Solís Neffa 692 (BAA, CTES, MNES, SI)
	40	4x	A. Misiones, Capital, Posadas. Hojsgaard 70 (MNES) ## MNES 303
	40	4x	A. Misiones, Montecarlo, Club de pesca. Hojsgaard 116 (MNES)
	40	4x	A. Misiones. Iguazú, P.N. Iguazú, Hojsgaard s/n°
	60**	6x	A. Misiones, Eldorado, Eldorado. Hojsgaard 275 (MNES) ## MNES 647
	60	6x	A. Misiones, San Ignacio, P.P. Teyú Cuaré. Hojsgaard 353 (MNES)
	60	6x	A. Misiones, G. San Martín, A° 3 de Mayo. Hojsgaard 175 (MNES) ## MNES 350
<i>P. conspersum</i> Schrad.	60	6x	A. Misiones, San Ignacio, Santo Pipó. Hojsgaard 194 (MNES)
	40	4x	A. Misiones, Capital, Miguel Lanús. Hojsgaard 323 (CTES, MNES) #
<i>P. dedecae</i> Quarin	40	4x	A. Formosa, Clorinda, Ruta Nac. 11, km 1272. Honfi 1070 (MNES)
<i>P. denticulatum</i> Trin.	40	4x	A. Formosa, Clorinda, Ruta Nac. 11, km 1272. Honfi 1071 (MNES)
	40	4x	A. Misiones, Capital, Posadas. Hojsgaard 256 (MNES, CTES)
	40	4x	A. Buenos Aires, San Cayetano, San Cayetano. Hojsgaard 149 (MNES) ## MNES 404
<i>P. dilatatum</i> Poir.	40	4x	A. Río Negro, Capital, Colonia Echarren. Hojsgaard 258 (MNES, CTES)
	40	4x	A. Misiones, Capital, Posadas. Hojsgaard 148 (MNES, CTES)
<i>P. distichum</i> L.	40	4x	A. Corrientes, Ituzaingó, Ituzaingó. Hojsgaard 278 (MNES)

Table 1 continued

Species	2n	x	Locality and vouchers
<i>P. ellipticum</i> Döll	80*	8x	A. Misiones, Capital, Miguel Lanús. Hojsgaard 320 (MNES, CTES)
<i>P. erianthoides</i> Lindm.	80*	8x	A. Misiones, Capital, Miguel Lanús. Hojsgaard 322 (MNES)
<i>P. falcatum</i> Nees ex Steud.	20	2x	A. Misiones, Candelaria, Corpus. Almada 74 (MNES, CTES)
	20	2x	A. Misiones, Candelaria, Arroyo Yabebiry margins. Honfi 882A. (MNES)
<i>P. glabrinode</i> (Hack.) Morrone et Zuloaga	20*	2x	A. Misiones, San Ignacio, Paraná River. Rua 177(BAA) # BAA 22866
<i>P. glaucescens</i> Hack.	20	2x	A. Misiones, Capital, Miguel Lanús. Hojsgaard 147 (MNES)
	40	4x	P. Amambay, 50 km S de Bella Vista. Rua 58 (BAA)
<i>P. guenoarum</i> Arechav.	40	4x	A. Misiones, Capital, Garupá. Hojsgaard 265 (MNES, CTES)
<i>P. humboldtianum</i> Flügge	20	2x	BO. Cochabamba, Chaparé, Miguelito. Rua 356 (BAA)
	40	4x	BO. Santa Cruz, Florida, Samaipata. Rua 315 (BAA) # BAA 23204
<i>P. inaequivalve</i> Raddi	60	6x	P. Paraguari, 2 km W de Carapeguá. Rua 209 (BAA)
	60	6x	A. Misiones, Capital, Posadas. Hojsgaard 145 (MNES, CTES) ## MNES 147
	60	6x	A. Misiones, G. San Martin, Gruta India. Hojsgaard 177 (MNES)
	60	6x	A. Misiones, San Pedro, P. P. Moconá. Hojsgaard 300 (MNES, CTES)
	60	6x	A. Misiones, San Pedro, P. P. Moconá. Hojsgaard 305 (MNES)
<i>P. indecorum</i> Mez	20	2x	A. Misiones, Capital, Nemesio Parma. Hojsgaard 244 (MNES, CTES)
	20	2x	A. Misiones, Apóstoles, San José. Hojsgaard 252 (MNES, CTES)
	20	2x	A. Misiones, Candelaria, Santa Ana. Honfi 1187 (MNES)
<i>P. intermedium</i> Munro ex Morong et Britton	20	2x	P. Amambay, 15 km S de Bella Vista. Rua 35 (BAA) # BAA 22649
<i>P. ionanthum</i> Chase	40	4x	P. Cordillera, Tobatí. Honfi 1177. (MNES)
<i>P. juergensii</i> Hack.	20	2x	A. Misiones, Capital, Posadas. Hojsgaard 53 (MNES)
	20	2x	A. Misiones, Capital, Miguel Lanús. Hojsgaard 146 (MNES, CTES) ## MNES 414
	20	2x	A. Corrientes, Ituzaingó, Garapé. Hojsgaard 165 (MNES, CTES) ## MNES 418
	20	2x	A. Corrientes, Ituzaingó, Garapé. Hojsgaard 167 (MNES, CTES) ## MNES 752
	20	2x	P. Itapúa, Encarnación. Hojsgaard 181 (MNES, CTES)
<i>P. lenticulare</i> Kunth	20	2x	A. Misiones, Apóstoles, San José. Hojsgaard 253 (MNES, CTES)
	40	4x	B. Mato Grosso, Ruta Transpantaneira, km 19. Rua 278 (BAA, L, MNES) # BAA 22967
<i>P. leptum</i> León (= <i>P. nicorae</i> Parodi)	40	4x	P. Cordillera, Tobatí. Honfi 1178 (MNES)
<i>P. lilloi</i> Hack.	20*	2x	A. Misiones, P.N. Iguazú, Cataratas del Iguazú. Rua 127 (BAA) # BAA 22741
	20	2x	A. Misiones, P.N. Iguazú, Cataratas del Iguazú. Hojsgaard 335 (MNES)
<i>P. limbatum</i> Henrard	20	2x	A. Misiones, Capital, Posadas. Hojsgaard 191 (MNES, CTES)
	20	2x	A. Misiones, Capital, Posadas. Hojsgaard 295 (MNES)

Table 1 continued

Species	2n	x	Locality and vouchers
<i>P. malacophyllum</i> Trin.	40	4x	BO. Santa Cruz, Caballero, Comarapa. Rua 333 (BAA, MNES) # BAA 23222
	40	4x	P. Amambay, P. N. Cerro Corá. Rua 298 (BAA, L, MNES) # BAA 22987
	40	4x	A. Misiones, Candelaria, P. P. Profundidad. Hojsgaard 284 (MNES)
	40	4x	A. Córdoba, Huerta Grande. Hojsgaard 292 (MNES)
	40	4x	A. Jujuy, Ledesma, P.N. Calilegua, Río Aguas Negras. Solis Neffa 710 (BAA, CTES, MNES, SI)
	40	4x	A. Jujuy, Ruta 34 y Río Yuto. Solis Neffa 759 (BAA, CTES, MNES, SI, US)
<i>P. mandiocanum</i> Trin. var. <i>subaequiglume</i> I. L. Barreto	60	6x	A. Misiones, Eldorado, Eldorado. Hojsgaard 274 (MNES)
<i>P. modestum</i> Mez	40	4x	A. Corrientes, Ruta Nac. 12 km 1263. Hojsgaard 279 (MNES) #
	40	4x	A. Corrientes, Itá Ibaté. Hojsgaard 333 (MNES, CTES)
<i>P. notatum</i> Flügge	40	4x	A. Corrientes, Paso de los Libres, La Cruz. Hojsgaard 327 (MNES, CTES)
<i>P. notatum</i> Flügge var. <i>saurae</i> Parodi	20	2x	B. Mato Grosso do Sul, Dourados. Rua 296 (BAA, L) # BAA 22985
<i>P. orbiculatum</i> Poir.	20	2x	P. Paraguari, Carapeguá, Ruta Nac. 1. Honfi 1073 (MNES)
<i>P. ovale</i> Nees ex Steud.	80*	8x	A. Misiones, Capital, Miguel Lanús. Rua 476 (BAA, MNES) # BAA 24339
	80	8x	A. Misiones, Capital, Miguel Lanús., Rua 478 (BAA, MNES) # BAA 24341
	80	8x	A. Misiones, Capital, Nemesio Parma. Hojsgaard 248 (MNES, CTES)
	80	8x	A. Misiones, Capital, Miguel Lanús. Hojsgaard 313 (MNES, CTES)
	80	8x	A. Misiones, Capital, Miguel Lanús. Hojsgaard 324 (MNES, CTES)
<i>P. paniculatum</i> L.	20	2x	A. Misiones, Capital, Posadas. Hojsgaard 71 (MNES)
	20	2x	A. Misiones, Capital, Garupá. Hojsgaard 261 (MNES, CTES)
	20	2x	A. Misiones, Capital, Miguel Lanús. Honfi 1068 (MNES)
	20	2x	A. Misiones, Candelaria, Cerro Santa Ana. Honfi 1188 (MNES)
<i>P. pauciciliatum</i> (Parodi) Herter	40	4x	A. Misiones, Capital, Posadas. Hojsgaard 65 (MNES, CTES)
	40	4x	P. Itapúa, Encarnación. Hojsgaard 184 (MNES)
	40	4x	A. Salta, Capital, rotonda de acceso Aeropuerto. Solís Neffa 838 (BAA, CTES, MNES, SI, US)
<i>P. paucifolium</i> Swallen	20**	2x	P. Paraguari, Villa Florida. Daviña 549 (MNES) ## MNES 440
<i>P. plicatum</i> Michx.	40	4x	A. Corrientes, Ituzaingó, Garapé. Hojsgaard 168 (MNES, CTES) ## MNES 401
	40	4x	A. Misiones, Candelaria, Profundidad. Hojsgaard 288 (MNES, CTES)
	40	4x	A. Córdoba, Huerta Grande. Hojsgaard 293 (MNES)
	40	4x	A. Misiones, Capital, Miguel Lanús. Hojsgaard 316 (MNES, CTES)
	40	4x	A. Misiones, Capital, Miguel Lanús. Hojsgaard 321 (MNES, CTES)

Table 1 continued

Species	2n	x	Locality and vouchers
<i>P. polyphyllum</i> Nees ex Trin.	40	4x	A. Misiones, Capital, Garupá. Hojsgaard 264 (MNES)
<i>P. quadrifarium</i> Lam.	30	3x	A. Buenos Aires, San Cayetano, San Cayetano. Hojsgaard 232 (MNES)
<i>P. quarinii</i> Morrone et Zuloaga	20	2x	A. Misiones, Apóstoles, San José. Hojsgaard 254 (MNES)
	20	2x	A. Misiones, Capital, Garupá. Hojsgaard 262 (MNES)
	20	2x	A. Misiones, Candelaria, Cerro Corá. Hojsgaard 290 (MNES)
	20	2x	A. Misiones, Candelaria, Cerro Santa Ana. Honfi 1190 (MNES, CTES)
<i>P. regnellii</i> Mez	40	4x	A. Misiones, P.N. Iguazú. Rua 464 (BAA, CTES, L) # BAA 23882
	40	4x	A. Misiones, Montecarlo, Club de pesca. Hojsgaard 117 (MNES)
	40	4x	A. Misiones, G. San Martín, A° 3 de Mayo. Hojsgaard 171 (MNES)
	40	4x	A. Misiones, G. San Martín, Gruta India. Hojsgaard 173 (MNES)
	40	4x	A. Misiones, G. San Martín, A° 3 de Mayo. Hojsgaard 179 (MNES) ## MNES 354
	40	4x	A. Misiones, Eldorado, Maria Magdalena. Hojsgaard 273 (MNES)
<i>P. remotum</i> J. Rémy	80*	8x	BO. Tarija, Tomatitas. Rua 543 (BAA)
	80	8x	A. Jujuy, Capital, Lozano. Solis Neffa 830 (BAA, CTES, MNES, SI)
	80	8x	A. Salta, La Caldera, ruta provincial 9, km 1654. Hojsgaard 379 (CTES)
<i>P. repens</i> P. J. Bergius	20	2x	A. Misiones, Capital, Nemesio Parma. Hojsgaard 271 (MNES, CTES)
<i>P. simplex</i> Morong	40	4x	P. Presidente Hayes, Puerto Falcón. Daviña 540 (MNES, CTES)
	40	4x	P. Presidente Hayes, Puerto Falcón. Daviña 541 (MNES, CTES)
<i>P. stellatum</i> Humb. et Bonpl. ex Flügge	32	–	A. Misiones, San Ignacio, P.P. Teyú Cuaré. Honfi 1168 (MNES, CTES) #
<i>P. umbrosum</i> Trin.	20	2x	P. Itapúa, Ruta Nac. 1, Encarnación. Daviña 554 (MNES, CTES)
<i>P. unispicatum</i> (Scribn. et Merr.) Nash	40	4x	A. Jujuy, Capital, Palpalá. Solis Neffa 826 (BAA, CTES, MNES, SI)
	40	4x	A. Salta, Capital, B° Grand Bourg. Solis Neffa 849 (CTES, MNES)
<i>P. urvillei</i> Steud.	40	4x	A. Corrientes, Ituzaingó, Aguape-í stream. Hojsgaard 154 (MNES, CTES)
	40	4x	A. Corrientes, Ituzaingó, Aguape-í stream. Hojsgaard 155 (MNES, CTES)
	40	4x	P. Itapúa, Encarnación. Hojsgaard 183 (MNES, CTES)
	40	4x	A. Misiones, Capital, Nemesio Parma. Hojsgaard 234 (MNES)
	40	4x	A. Misiones, Candelaria, P. P. Profundidad. Hojsgaard 285 (MNES, CTES)
	40	4x	A. Misiones, San Ignacio, P. P. Teyú Cuaré. Honfi 1173 (MNES, CTES, SI) #
<i>P. usteri</i> Hack.	40	4x	A. Misiones, San Ignacio, P. P. Teyú Cuaré. Honfi 1174 (MNES) #
	40	4x	A. Misiones, San Ignacio, P. P. Teyú Cuaré. Honfi 1175 (MNES) #
	40	4x	P. Cordillera, San Bernardino, LagoYpacaraí. Rua 10 (BAA) # BAA 22624
<i>P. vaginatum</i> Sw.	40	4x	P. Presidente Hayes, camino M. Roque Alonso a Clorinda. Rua 304 (BAA)

Table 1 continued

Species	2n	x	Locality and vouchers
<i>P. virgatum</i> L.	40	4x	B. Mato Grosso, 1 km W of Chapada dos Guimarães. Rua 246 (BAA)
	40	4x	BO. Cochabamba, Chapare, camino Miguelito a Villa Tunari. Rua 358 (BAA) # BAA 23248
	40	4x	B. Mato Grosso, camino a Rondonópolis, km BR 364. Rua 293 (BAA) # BAA 22982
	40	4x	BO. Santa Cruz, Ñufla de Chávez, Los Troncos. Rua 366 (BAA) # BAA 23256
<i>P. wrightii</i> Hitchc. et Chase	20	2x	B. Mato Grosso, camino a Porto Cercado, km 9. Rua 284 (BAA)
	40	4x	B. Mato Grosso, Ruta Transpantaneira, km 11. Rua 271 (BAA) # BAA 22960
	40	4x	A. Corrientes, Itá Ibaté, Río Paraná. Hojsgaard 328 (MNES, CTES)

Code for Herbaria (Holmgren and Holmgren 1998): BAA ‘Gaspar Xuárez’ Universidad de Buenos Aires, Argentina; CTES Instituto de Botánica del Nordeste, Corrientes, Argentina; MNES Universidad Nacional de Misiones, Posadas, Argentina; L Nationaal Herbarium Nederland—Leiden University, Leiden, Netherlands; SI Instituto de Botánica Darwinion, San Isidro, Argentina and US Smithsonian Institution, Washington DC, USA

*, First somatic chromosome number; **, New record, #, Currently cultivated alive materials identified by its voucher number or by its respective accession numbers into the experimental garden; ##, Materials with seed samples preserved at 4°C identified by its respective accession numbers into the seed collection

A Argentina; **B** Brazil; **BO** Bolivia; **P** Paraguay

macerated in a drop of 2% aceto-orcein and then squashed. Coverslips were removed by freezing with liquid CO₂, and permanent slides were made by using DEPEX or euparal as a mounting medium (Bowen 1956).

Results and discussion

The somatic chromosome numbers and ploidy levels of 131 accessions belonging to 55 *Paspalum* species, mainly from Argentina, are reported. First chromosome counts for six species, and chromosome numbers differing from those previously reported for five species are provided (Table 1). Some selected squashed cells are illustrated in Figs. 1, 2, and chromosomal novelties are discussed below.

Diploids

Somatic chromosome numbers for *Paspalum lilloi* Hack. and *P. glabrinode* (Hack.) Morrone et Zuloaga are reported for the first time. Both species have $2n = 2x = 20$ (Fig. 1a, b) and limited geographical distributions. *Paspalum lilloi* grows on humid rocky

slopes, riverine margins, rapids and waterfalls. Currently, this species is now limited to a restricted area surrounding the Iguazú National Parks (Argentina, Brazil), because hydrological conditions have been altered by dam construction on the Paraná River. *Paspalum glabrinode* is only known from northeastern Argentina and neighbouring regions in Brazil and Paraguay (Zuloaga and Morrone 2005). Recently, the meiotic behaviour of *P. glabrinode* was studied by Morrone et al. (2006), who reported diploidy based on ten bivalents observed at metaphase I. We confirm the diploid condition for this taxon.

We found a new ploidy level for *P. paucifolium* Swallen ($2n = 2x = 20$, Fig. 1c), a species with good potential as an animal forage (Barreto 1974) that we found growing in nature on sandy and rocky dry soils in Paraguay and collected from Paraguari Department. Burson (1997) reported two tetraploid, facultative aposporous, apomictic accessions from Brazil; this new diploid cytotype is expected to reproduce sexually as all known diploids in the genus do. If this is the case, this germplasm will be interesting for crop improvement.

Paspalum almum Chase is either considered as member of the informal group “Notata” (Barreto

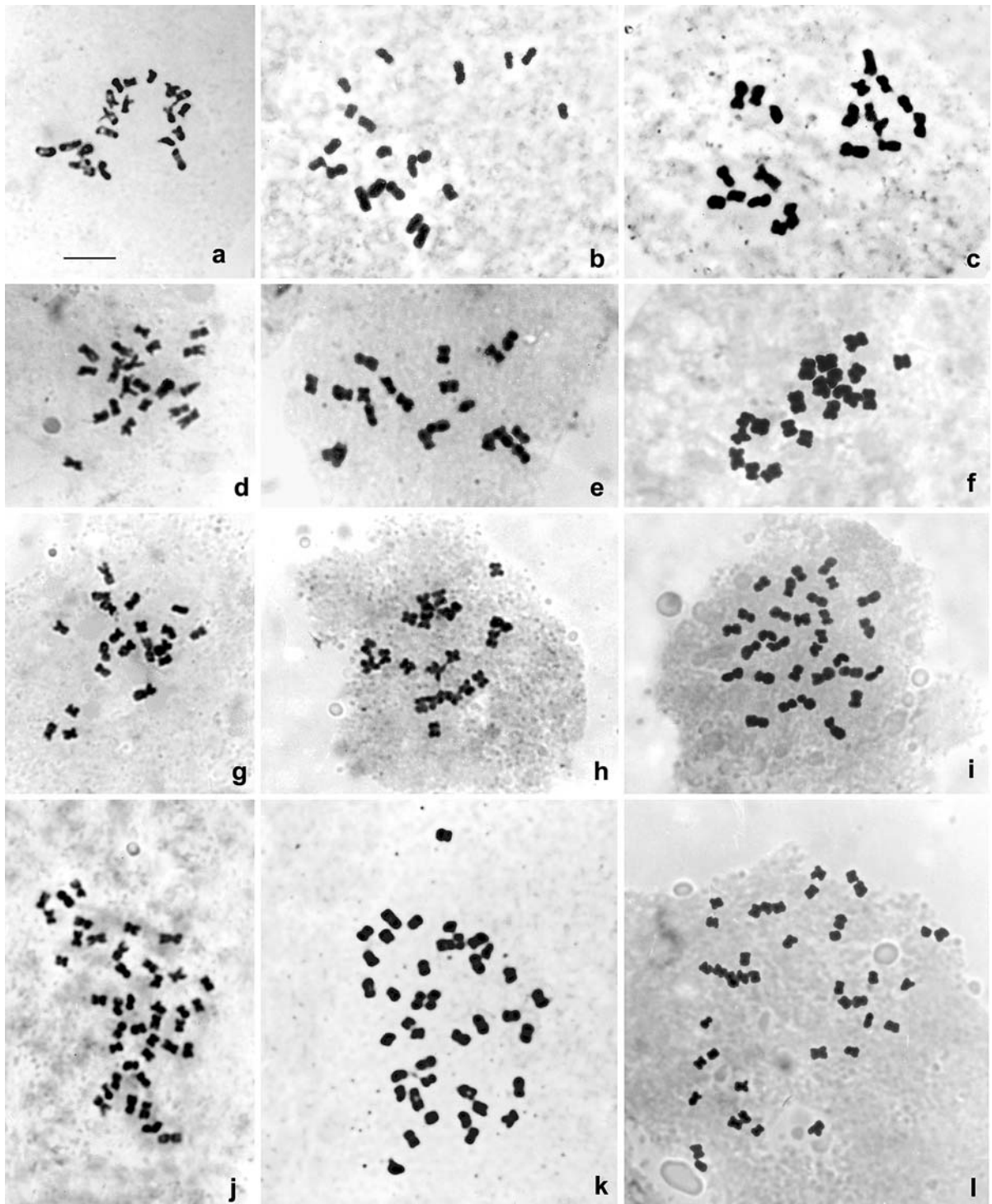


Fig. 1 Somatic chromosomes. **Diploids** ($2n = 2x = 20$). **a** *Paspalum lilloi* (Hojsgaard 335). **b** *P. glabrinode* (Rua 177). **c** *P. paucifolium* (Daviña 549). **d** *P. repens* (Hojsgaard 271). **e** *P. humboldtianum* (Rua 356). **f** *P. indecorum* (Hojsgaard 252). **g** *P. quarinii* (Hojsgaard 254). **h** *P. falcatum*

(Almada 74). **Triploid** ($2n = 3x = 30$). **i** *P. quadrifarium* (Hojsgaard 232). **Tetraploids** ($2n = 4x = 40$). **j** *P. plicatulum* (Hojsgaard 293). **k** *P. dilatatum* (Hojsgaard 149). **l** *P. unispicatum* (Solis Neffa 849). Scale bar = 5 μm

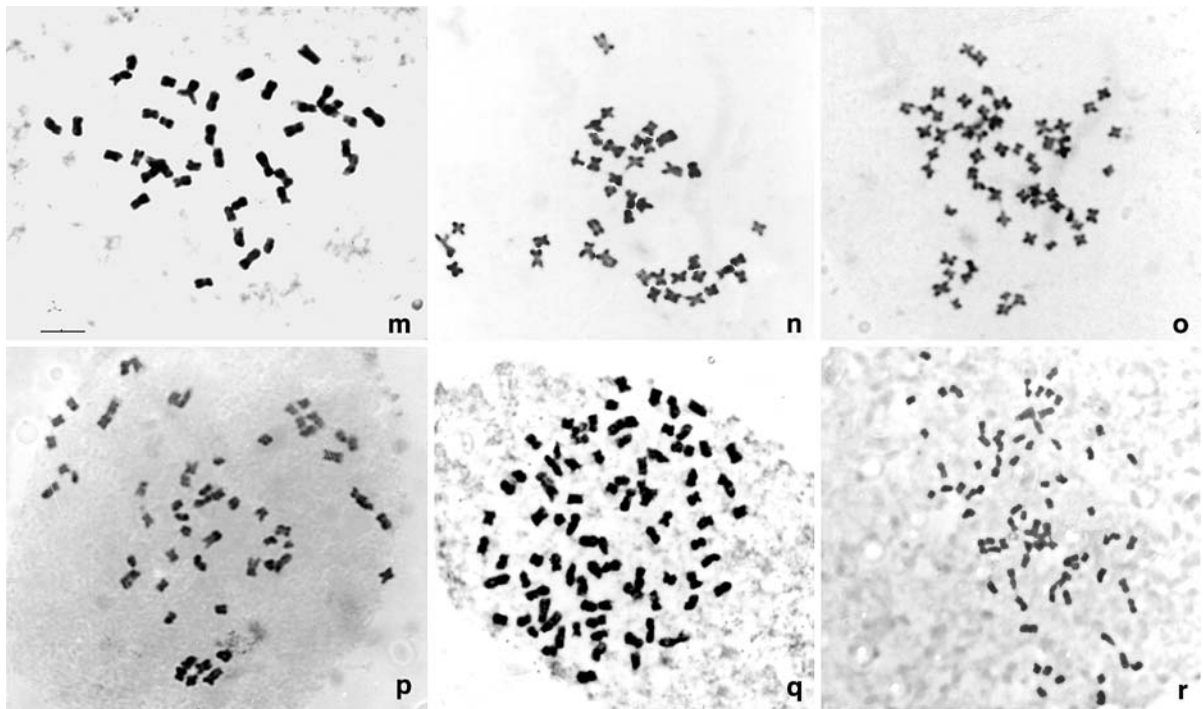


Fig. 2 Somatic chromosomes. **Tetraploids** ($2n = 4x = 40$). **m.** *Paspalum regnellii* (Rua 464). **n** *P. malacophyllum* (Hojsgaard 292). **Hexaploids** ($2n = 6x = 60$). **o** *P. inaequivalve* (Hojsgaard

300). **p** *P. conjugatum* (Hojsgaard 275). **Octoploids** ($2n = 8x = 80$). **q** *P. ovale* (Hojsgaard 248). **r** *P. remotum* (Solis Neffa 830). Scale bar = 5 μ m

1957, 1974; do Canto-Dorow et al. 1996) or proposal as a different group, “Alma” (Quarin 1974; Zuloaga et al. 2004). This species has a sexual diploid cytotype ($2n = 2x = 12$, sub *P. hexastachyum* Parodi) and tetraploids ($2n = 4x = 24$) that reproduces by apomixis (Bashaw et al. 1970; Quarin 1974; Burson 1975; Quarin and Hanna 1980) and our chromosome results agree with these works. Most of *Paspalum* species have the basic number of chromosomes $x = 10$, however in very few species were reported other exceptional numbers, such as $x = 6$ in *P. almum* (Quarín 1974), $x = 9$ for *P. lanciflorum* Trin. (sub *P. contractum* Pilg., Davidse and Pohl 1974) and $x = 16$ for *P. convexum* Humb. Bonpl. ex Flüggé (Selva 1976; Reeder 1984). Recently, Peñalosa et al. (2008), have reported chromosome numbers of five species with unexpected $2n = 18, 24, 36$, and 48, which could be multiple to $x = 6$ or $x = 9$.

Tetraploids

The most frequent ploidy level among these collections was tetraploidy, and all counts agree with

previous reports (Davidse and Pohl 1972, 1974, 1978; Honfi et al. 1990; Norrmann et al. 1994a; Hunziker et al. 1998; Pagliarini et al. 2001; Urbani et al. 2002; Adamowski et al. 2005; Morrone et al. 2006; Souza-Chies et al. 2006; Essi and Souza-Chies 2007; Pozzobon et al. 2000, 2008 and references therein) (Figs. 1j–l, 2m–n). The tetraploid condition in *Paspalum* embraces both sexual and apomictic modes of reproduction. Most apomictic tetraploids have sexual, diploid conspecific counterparts, e.g. the $4x$ chromosome races of *P. almum*, *P. notatum* and *P. plicatulum* Michx. (Burton 1948; Bashaw et al. 1970; Quarin and Hanna 1980; Espinoza and Quarin 1997). However, sexually reproducing tetraploids are also found in some *Paspalum* species, in which they are found either as a single condition for a taxon or as one component of an agamic polyploid complex with higher ploidy levels. The genetic systems of *P. regnellii* Mez (Norrmann 1981), *P. urvillei* Steud. (Bashaw et al. 1970) and *P. virgatum* L. (Burson and Quarin 1982) are based on allotetraploidy and sexual reproduction, without the coexistence of cytotypes having different ploidy levels. A different genetic

system occurs in *P. dilatatum* in which allopolyploidy at tetraploid level is also associated with sexual reproduction but conspecific allohexaploid and allohexaploid apomictic races also exist (Burson 1983). Moreover, several biotypes of each ploidy level of *P. dilatatum* were recognized by its morphology, cytology and reproductive behaviour (Burson 1983, 1995) and also by molecular methods (Speranza 2005; Speranza and Malosetti 2007; Miz and Souza-Chies 2006 and references therein). *Paspalum ionanthum* Chase resulted also tetraploid ($2n = 4x = 40$), however it is an exceptional species because have sexual cross-pollinated tetraploids and also co-specific apomictic octoploids instead most of $4x$ of *Paspalum* are autogamous (sub *P. guaraniticum* Parodi, Burson and Bennett 1970; Quarin and Norrmann 1987b).

Hexaploids

A new chromosome number for *Paspalum ceresia* ($2n = 6x = 60$) is reported here. This taxon belongs to subgenus *Ceresia* (Pers.) Rchb., in which hexaploidy had been previously reported only for *P. pectinatum* Nees ex Trin. (Gould and Soderstrom 1967). *Paspalum ceresia* (Kuntze) Chase comprises two ploidy levels, with tetraploids found in northwestern Argentina (Morrone et al. 2006) and hexaploids in Bolivia.

For *P. conjugatum* P. J. Bergius, we found two chromosome races ($2n = 4x = 40$ and $2n = 6x = 60$), the hexaploid cytotype (Fig. 2p) newly reported. The $4x$ and $6x$ races are sympatric at our collection localities. Hexaploids can be distinguished by some morphological differences, i.e. larger plants, spikelets and racemes, from the tetraploids. Our finding agrees with a single hexaploid previously found by C. Quarin (Pers. comm.). In *P. conjugatum*, diploids ($2n = 20$), tetraploids ($2n = 40$) and octoploids ($2n = 80$) were previously reported (Hsu 1967; Gould and Soderstrom 1974; Dujardin 1978; Honfi et al. 1990). The hexaploid condition found here completes the polyploid series for this taxon and represents a new chromosome race for South American accessions, since only tetraploids had been previously found in this continent. Studies on meiotic behaviour and molecular markers can reveal if this hexaploid cytotype has an autoploid origin.

A new ploidy level for *P. alcalinum* Mez ($2n = 6x = 60$) was also found. Burson (1997) noted Paraguayan accessions with diploid, tetraploid, and

pentaploid levels. Material of *P. alcalinum* from South America has been repeatedly misidentified as *P. hartwegianum* E. Fourn., a closely related species restricted to Mexico and also hexaploid (Gould 1958; Davidse and Pohl 1972; Zuloaga and Morrone 2005; Morrone et al. 2006). A detailed taxonomic revision is needed to clarify the taxonomic identity of material reported as *P. hartwegianum* $6x$ from Brazil by Pozzobon et al. (2000).

Octoploids

Four species with this ploidy level were found. Although ploidy levels vary within the genus from $2x$ to $16x$, octoploidy is only known in 13 *Paspalum* species including the four taxa mentioned below. None of these species had been previously studied reproductively. The chromosome number $2n = 8x = 80$ is the first one reported for *P. erianthoides* Lindm., a species inhabiting marshy soils of southwestern Brazil, eastern Paraguay and northeastern Argentina (Quarin 1975).

In *P. ellipticum* Döll from Brazil the gametic chromosome number $n = 40$ has been previously reported (Fernández et al. 1974), and a diploid chromosome race ($2n = 2x = 20$) was also found in this taxon (Souza-Chies et al. 2006). We confirm Fernández et al. (1974) by reporting the somatic chromosome number $2n = 80$ for this species.

All our accessions of *P. ovale* Nees ex Steud. were octoploids ($2n = 8x = 80$, Fig. 2q), as previously suggested by Saura (1941), sub *P. epile* Parodi, based on meiotic observations. This species comprises two high polyploid levels: octoploidy and heptaploidy ($2n = 7x = 70$), the latter found in Brazilian materials (Souza-Chies et al. 2006).

Paspalum remotum J. Rémy had $2n = 8x = 80$ chromosomes, (Fig. 2r) in agreement with a report of 40 bivalents observed in pollen mother cells at diakinesis and metaphase I by Hunziker et al. (1998).

Other ploidy levels

In *Paspalum* four odd ploidy levels have been previously reported, however, the triploids and pentaploids are those that commonly are in the nature (Honfi 2003). On the analysis of 933 antecedents of registered chromosomal numbers for 167 species of *Paspalum*,

Honfi (2003) found that odd natural polyploids are uncommon in the genus and that the levels of odd ploidy that have been found naturally includes triploidy ($3x$), pentaploidy ($5x$), heptaploidy ($7x$) and eneaploidy ($9x$), and that in all the cases they refer to species with $x = 10$. The natural odd ploidy levels in *Paspalum* are not easily found although a favorable context exists for its existence. In *Paspalum quadrifarium* Lam. we find $2n = 3x = 30$ (Fig. 1i) and this cytotype is the most widely distributed in the nature, instead diploid and tetraploid co-specific counterparts of this species, are geographically restricted (Quarin and Lombardo 1986; Norrmann et al. 1989). All provenances of *P. aff. arundinellum* Mez are pentaploids and this agrees with previous reports (Honfi et al. 1990; Honfi 2003) with the exception of an aneuploid condition ($2n + 1 = 5x + 1 = 51$) found in one accessions from Argentina.

Cytogeographical biodiversity

New geographical records of ploidy levels were found in three countries. *Paspalum orbiculatum* Poir. and *P. umbrosum* Trin. ($2x$) and *P. arundinellum* Mez ($4x$) accessions are new for Paraguay, *P. modestum* Mez ($4x$) for Argentina, and *P. humboldtianum* Flügge ($4x$) and *P. remotum* ($8x$) for Bolivia.

Quarin (1992) described a polyploidization and gene-flow model for several *Paspalum* species. The system comprises sexual diploids and their apomictic, tetraploid conspecific counterparts, with triploids acting as potential gene-flow bridges between them (Quarin 1992; Norrmann et al. 1994b; Espinoza and Quarin 1997). Genetic variability of sexual diploids would be naturally transferred to higher ploidy levels. New autotetraploid genotypes are likely produced in nature through fertilisation of unreduced, $2n$ gametes of diploids by functional, reduced male gametes, produced in abundance by apomictic tetraploids (Espinoza and Quarin 1997). In this way, diploids are involved in the generation of genetic variability within apomictic, tetraploid *Paspalum* species. Recently, Daurelio et al. (2004) studied the variability of natural populations of *P. notatum* consisting of plants of either a single ploidy level or co-habiting $2x$ and $4x$ races. In agreement with Quarin's model for interploidy gene flow in *Paspalum*, comparisons between apomictic tetraploid populations belonging to allopatric or sympatric populations in relation to

their diploid counterparts, revealed that genotypic diversity is higher in populations where tetraploids grow in the vicinity of their conspecific sexual diploids. Since breeding programs focused on apomictic polyploid grasses are looking for new apomictic genotypes, knowledge about regions where chromosome races are sympatric represents an important reference for collecting and/or preserving genetic variability in nature.

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