

# Chromosome number and ploidy level of some South American species of *Schizachyrium* (Poaceae, Andropogoneae)

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**Abstract** Chromosome numbers are reported here for 53 accessions belonging to 13 taxa of the genus *Schizachyrium*. The chromosome counts for the following seven species are recorded here for the first time: *S. bimucronatum* ( $2n = 20$ ), *S. gracilipes* ( $2n = 20$ ), *S. hatschbachii* ( $2n = 20$ ), *S. lactiflorum* ( $2n = 20$ ), *S. plumigerum* ( $2n = 20$ ), *S. salzmannii* ( $2n = 20$ ;  $2n = 40$ ) and *S. spicatum* ( $2n = 20$ ). Counts differing from those previously reported are given for two species: *S. scabriflorum* ( $2n = 20$  and  $80$ ) and *S. tenerum* ( $2n = 40$ ). Most of the analyzed species of this genus are diploids. The occurrence of polyploidy in *S. glaziovii*, *S. lactiflorum*, *S. salzmannii*, *S. scabriflorum* and *S. tenerum* is reported here for the first time. Data on chromosome numbers and ploidy levels are discussed in relation to the taxonomy and evolution of the genus.

**Keywords** Chromosome numbers · Grasses · Polyploidy · Taxonomy · *Schizachyrium*

## Introduction

The genus *Schizachyrium* Nees belongs to the tribe Andropogoneae Dumort and comprises 50–60 species that are distributed in tropical and subtropical regions of the world, mostly in Africa and America (Clayton and Renvoize 1986; Nicora and Rúgolo de Agrasar 1987), where

the genus is represented by 24 and 30 species, respectively (Clayton and Renvoize 1986; Peichoto 2007).

For South America, Filgueiras (2003) and Peichoto (2010) have recognized 19 species of *Schizachyrium*. These species are important components of South American natural grasslands and savannas which usually have little moisture, although some of them also live in prairies around woodlands, and even in temporarily humid lands. In South America, the genus achieves its greatest diversity in the subtropical region, with some species reaching the temperate zones of Argentina, Brazil and Uruguay. Recently, South American species of *Schizachyrium* have been the subject of renewed taxonomic and evolutionary interest since the taxonomy of this group of species is controversial as a consequence of the doubtful identity of some taxa as well as the great morphological and ecological variability of other species of the genus (Peichoto 2007, 2010; Peichoto et al. 2008).

Because chromosome data have often clarified the evolutionary and taxonomic relationships in plants (Sanders 1987; Carr et al. 1999; Solís Neffa and Fernández 2000), we are currently carrying out a comprehensive study of the chromosome numbers and ploidy levels in South American species of *Schizachyrium*. In this sense, the data available for the genus provide a good representation of African (De Wet 1954; Dujardin 1978, 1979; Kammacher et al. 1973; Olorode 1974; Spies and Du Plessis 1987), Asian (Tateoka 1955; Gould and Soderstrom 1974; Mehra and Kalia 1974; Dujardin and Bryne 1975; Kalia 1978; Mehra 1982; Christopher and Samraj 1985), European (Krupko 1953), Central American (Davidse and Pohl 1972, 1974; Pohl and Davidse 1971) and North American taxa (Carman and Hatch 1982; Brown 1950, 1951; Bruner 1987; Church 1936; Gould 1956, 1968; Hatch 1975). The chromosome numbers previously reported for 30 of these species vary

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greatly, from  $2n = 20$  to  $2n = 100$ . Nevertheless, the most common chromosome numbers are  $2n = 2x = 20$  (35%) and  $2n = 4x = 40$  (40%), all of them showing the basic number  $x = 10$ .

Despite the several counts in the genus *Schizachyrium*, scarce information is available on chromosome numbers and ploidy levels of South American species. To our knowledge, chromosome numbers have so far been determined for only three species: *S. scabriflorum* (Rupr. ex Hack.) A. Camus, which has been reported as tetraploid ( $2n = 4x = 40$ ) (Killeen 1990), *S. microstachyum* (Desv. ex Ham.) Roseng., B.R.Arrill. and Izag., which has been documented as diploid ( $2n = 2x = 20$ ) (Saura 1948; Gould 1956; Killeen 1990), and *S. sanguineum* (Retz.) Alston, which has been reported to show different ploidy levels (Killeen 1990; Norrmann et al. 1994).

Thus, with the aim of increasing the cytological knowledge of South American species of *Schizachyrium*, in the present study we report the chromosome numbers and ploidy levels of 53 accessions belonging to 13 species. The results are discussed in relation to the taxonomy and evolution of the genus.

## Materials and methods

The specimens studied were collected in northeastern Argentina (Corrientes, Entre Ríos and Misiones provinces). Some plants were gathered in Paraguay (Amambay, Cordillera and Guairá departments). The taxa were identified following the criteria proposed by Peichoto (2010). Voucher specimens were deposited at CTES herbarium (Holmgren et al. 1990).

Some plants were cultivated in a greenhouse of the Facultad de Ciencias Agrarias (Universidad Nacional del Nordeste), Corrientes, Argentina. A complete list of the taxa analyzed and the origin of the accessions are provided in Table 1.

The ploidy level of the plants sampled was inferred from chromosome counts and estimates of the relative DNA content using flow cytometry. The chromosome counts were obtained from mitotic material gathered from greenhouse-grown plants. Chromosome preparations were obtained from squashes of root tips taken from potted plants. Root tips were collected between 8:00 and 10:00 a.m. and were then pretreated for 2 h in alpha-bromonaphthalene solution at room temperature. Subsequently, the material was hydrolyzed in 1 N HCl at 60°C for 10 min and stained using the Feulgen technique.

Flow cytometry analyses were used to determine the ploidy level for some plants using leaf tissue and following the recommendations in the Partec kit CyStain UV Precise P (05-5002) manual, which was used to

prepare the samples. Briefly, 0.5 cm<sup>2</sup> of leaf material was placed on a petri dish with a comparable amount of tissue from an internal standard (P 60). After adding 0.5 ml of extraction buffer (Partec P kit CyStain UV Precise P 05-5002), the tissue was chopped with a razor blade. Following a 2-min incubation, samples were filtered through a 50-µm nylon mesh into the sample tube, and 1.5 ml of DAPI (4',6-diamidino-2-phenylindole) staining solution (Partec P kit CyStain UV Precise P 05-5002). The mixture was incubated for 2 min at room temperature and analyzed. The fluorescence intensity of DAPI-stained nuclei was determined using a Partec PA II flow cytometer (Partec, Münster, Germany) with the detector operating at 355 nm. About 3,000 nuclei were measured in each sample. Ploidy levels were estimated by comparing the DNA peak of the samples with the internal standard. The data were analyzed using PA II's Partec FloMax software.

## Results and discussion

A total of 53 ploidy level estimates were obtained for 13 South American taxa of the genus *Schizachyrium* (Table 1). The ploidy levels of seven of these taxa are reported here for the first time; two of the taxa yielded ploidy levels that have not been reported previously; the remaining four taxa confirmed previous reports. The results reported here confirm the basic number  $x = 10$  for the genus *Schizachyrium*, in agreement with the basic number proposed for most genera of Andropogoneae (Gould 1956).

*Schizachyrium bimucronatum* Roseng., B.R.Arrill. & Izag All the accessions analyzed from Argentina and Paraguay were diploid ( $2n = 2x = 20$ ; Figs. 1a and 2a). To our knowledge, this is the first report for this species, which is endemic to northeastern Argentina and Paraguay.

*Schizachyrium condensatum* (Kunth) Nees This species occurs mainly in America (Clayton and Renvoize 1986). In South America, it has been found in Argentina, Bolivia, Brazil, Colombia, Ecuador, Paraguay, Peru and Uruguay (Peichoto 2010). In the revision of the genus for South America, Türpe (1984) included *S. bimucronatum*, *S. lactiflorum* (Hack.) Herter, *S. microstachyum*, and *S. plumigerum* (Ekman) Parodi under *S. condensatum*. In disagreement with this, Peichoto et al. (2008) recognized all these taxa as different species. To our knowledge, there are only two previous studies dealing with the chromosome number of *S. condensatum* from Costa Rica (Pohl and Davidse 1971) and Mexico (Bruner 1987), which showed diploids and tetraploids, respectively. Although identified as *S. condensatum*, these counts are presumed to represent *S. microstachyum* and *S. condensatum sensu stricto* based

**Table 1** Chromosome numbers, ploidy levels and collection data of the 53 accessions of *Schizachyrium*, belonging to the 13 species

Species	2n	Ploidy level	Herbarium voucher numbers <sup>a</sup> and localities of collections
<i>S. bimucronatum</i>	20 <sup>b</sup>	2x	<i>P 76</i> – Argentina. Corrientes, Paso Naranjito, route 118
	20 <sup>b</sup>	2x	<i>P 87</i> – Argentina. Corrientes, route 14, between La Cruz and Yapeyú
	20 <sup>b</sup>	2x	<i>P 90</i> – Argentina. Corrientes, route 14, 5 km S of Yapeyú
	–	2x <sup>b</sup>	<i>P 138</i> – Argentina. Corrientes, route 14, 28 km N of Gobernador Virasoro
	20 <sup>b</sup>	2x	<i>P 103</i> – Argentina. Misiones, route 12, 16.5 km NE of Candelaria
	20 <sup>b</sup>	2x	<i>P 115</i> – Argentina. Entre Ríos, access to Concordia, 15 km W of Concordia
	20 <sup>b</sup>	2x	<i>P 123</i> – Paraguay. Cordillera, Tobatí
<i>S. condensatum</i>	20	2x	<i>P 54</i> – Argentina. Misiones, route 14, 10 km E of San José
	20	2x	<i>P 94</i> – Argentina. Corrientes, route 123, 2 km NW of Chavarría
	20	2x	<i>P 96</i> – Argentina. Corrientes, road to Virasoro, route 38
	20	2x	<i>P 106</i> – Argentina. Corrientes, route 118, 1 km E of Paso Naranjito
<i>S. glaziovii</i>	20	2x	<i>P 64</i> – Argentina. Corrientes, route 12, 1 km S of Riachuelo stream
	20	2x	<i>P 97</i> – Argentina. Misiones, 18 km NW of Concepción de la Sierra
	20	2x	<i>P 100</i> – Argentina. Misiones, route of Alem to Santa Ana, 14 km NW of Alem.
	20	2x	<i>P 112</i> – Argentina. Entre Ríos, 16 km W of Santa Ana
	–	3x <sup>b</sup>	<i>P 135</i> – Argentina. Misiones, Apóstoles, route 14, 12 km E of San José
	–	3x <sup>b</sup>	<i>P 145</i> – Argentina. Corrientes, Santo Tomé, route 120, 39 km NW of Gobernador Virasoro
	<i>S. gracilipes</i>	20 <sup>b</sup>	2x
<i>S. hatschbachii</i>	–	2x <sup>b</sup>	<i>P 131</i> – Argentina. Misiones, San Pedro, route 17 towards Bernardo de Irigoyen, 59 km E of crossroads between routes 17 and 120
<i>S. lactiflorum</i>	20 <sup>b</sup>	2x	<i>P 62</i> – Argentina. Corrientes, Route 12, 10.5 km W of access to Ituzaingó
	20 <sup>b</sup>	2x	<i>P 80</i> – Argentina. Corrientes, Route 118, between Paso Naranjito and Tatacuá
	20 <sup>b</sup>	2x	<i>P 118</i> – Paraguay. Departament of Cordillera, Tobatí
	–	3x <sup>b</sup>	<i>P 140</i> – Argentina. Corrientes, Ituzaingó, route 12, 9 km W of access to Ituzaingó
<i>S. microstachyum</i>	20	2x	<i>P 55</i> – Argentina. Misiones, 10 km E of San José, route 14
	20	2x	<i>P 82</i> – Argentina. Corrientes, road to Concepción, 5 km E of Santa Rosa
	20	2x	<i>P 117</i> – Argentina. Entre Ríos, access to Concordia, 12 km W of Concordia
<i>S. plumigerum</i>	20 <sup>b</sup>	2x	<i>P 68</i> – Argentina. Corrientes, Bella Vista
	–	2x	<i>P 113</i> – Argentina. Entre Ríos, 14 km N of Santa Ana
<i>S. salzmannii</i>	20 <sup>b</sup>	2x	<i>P 108</i> – Argentina. Corrientes, route 14, 26 km S of Curuzú Cuatiá
	–	2x	<i>P 157</i> – Argentina. Corrientes, 19 km W of western access to Ituzaingó
	40 <sup>b</sup>	4x	<i>P 61</i> – Argentina. Corrientes, route 12, 7 km W of access to Ituzaingó
	40 <sup>b</sup>	4x	<i>P 67</i> – Argentina. Corrientes, 12 km S of Bella Vista, route 27
<i>S. sanguineum</i>	40 <sup>b</sup>	4x	<i>P 120</i> – Paraguay. Amambay, route 3, 8 km S of Bella Vista
	40	4x	<i>P 69</i> – Argentina. Corrientes, Bella Vista.
	–	4x	<i>P 148</i> – Argentina. Misiones, route 105, near Estancia Santa Inés
	–	4x	<i>P 154</i> – Argentina. Corrientes, 31 km W of the limit between Corrientes and Misiones provinces
	50	5x	<i>P 81</i> – Argentina. Corrientes, road to Concepción, 5 km E of Santa Rosa
	50	5x	<i>P 102</i> – Argentina. Misiones, route 12, 16.5 km NE of Candelaria.
	80	8x	<i>P 78</i> – Argentina. Corrientes, between Paso Naranjito and Tatacuá, route 118
<i>S. scabriflorum</i>	20 <sup>c</sup>	2x	<i>P 60</i> – Argentina. Misiones, route 14, 10 km E of San José
	–	3x <sup>b</sup>	<i>P 137</i> – Argentina. Corrientes, Ituzaingó, route 14, 28 km N of Gobernador Virasoro
	–	3x <sup>b</sup>	<i>P 136</i> – Argentina. Misiones, Apóstoles, route 14, 12 km E of San José
	–	6x <sup>b</sup>	<i>P 152</i> – Argentina. Corrientes, Ituzaingó, 3 km W of the limit between Corrientes and Misiones provinces
	–	6x <sup>b</sup>	<i>P 144</i> – Argentina. Corrientes, Santo Tomé, route 120, 39 km NW of Gobernador Virasoro
	80 <sup>c</sup>	8x	<i>P 104</i> – Argentina. Misiones, route 12, 5 km NE of Candelaria

**Table 1** continued

Species	2n	Ploidy level	Herbarium voucher numbers <sup>a</sup> and localities of collections
<i>S. spicatum</i>	20 <sup>b</sup>	2x	<i>P 99</i> – Argentina. Misiones, 14 km NW of Alem, route Alem to Santa Ana
	20 <sup>b</sup>	2x	<i>P 110</i> – Argentina. Corrientes, 30 km N of Mocoretá, route 14
	20 <sup>b</sup>	2x	<i>P 111</i> – Argentina. Entre Ríos, 2 km W of Chajarí, road to Santa Ana
	–	2x	<i>P 149</i> – Argentina. Misiones, route 105, 6 km E of crossroads between routes 12 and 105
<i>S. tenerum</i>	40 <sup>c</sup>	4x	<i>P 79</i> – Argentina. Corrientes, route 118, between Paso Naranjito and Tatacuá
	60	6x	<i>P 92</i> – Argentina. Corrientes, 40 km NW of crossroads of routes 14 and 123
	–	6x	<i>P 132</i> – Argentina. Misiones, San Pedro, route 17 towards Bernardo de Irigoyen, 59 km E of crossroads between routes 17 and 120
	–	6x	<i>P 143</i> – Argentina. Corrientes, Santo Tomé, route 20, 39 km NW of Gobernador Virasoro

<sup>a</sup> *P* Peichoto

<sup>b</sup> First count for the taxon

<sup>c</sup> Count different from previous reports

on their geographic source. The four accessions from Northeastern Argentina were diploid.

*Schizachyrium glaziovii* Peichoto This species is also widespread in South America (Peichoto 2010). Prior to detailed studies of its inflorescence traits (Peichoto et al. 2008), *S. glaziovii* was treated as a subspecies of *S. microstachyum* (Rosengurt et al. 1968). Although not identified to subspecies, some chromosome numbers for *S. microstachyum* have been previously reported (Saura 1948; Gould 1956; Davidse and Pohl 1974). If such chromosome counts correspond to *S. glaziovii*, the somatic chromosome number  $2n = 2x = 20$  (Fig. 1b) presented here in four accessions would confirm previous data, while the ploidy level  $2n = 3x = 30$  (Fig. 2b) detected in another two accessions constitutes the first reports for this species.

*Schizachyrium gracilipes* (Hack.) A. Camus This species is a South American species distributed in northeastern Argentina, southern Brazil, Paraguay and Uruguay (Filgueiras 2003; Peichoto 2010). This species is one of the endemic taxa from northeastern Argentina, Paraguay and southern Brazil. The chromosome number  $2n = 2x = 20$  (Fig. 1c) found in the Paraguayan accession analyzed here is the first chromosome number reported for this species.

*Schizachyrium hatschbachii* Peichoto This species is one of the endemic taxa from southern Brazil, northeastern Argentina and Paraguay (Peichoto and Keller 2008; Peichoto 2010). Our ploidy level estimation is the first for this species and reveals that *S. hatschbachii* is diploid.

*Schizachyrium lactiflorum* This species is also an endemic to northeastern Argentina, Paraguay and southern Brazil (Peichoto 2010). This is the first report for this species. The Argentinian accessions were diploid ( $2n = 2x = 20$ ; Fig. 1d) and triploid ( $2n = 3x = 30$ ), whereas the Paraguayan accessions were diploid.

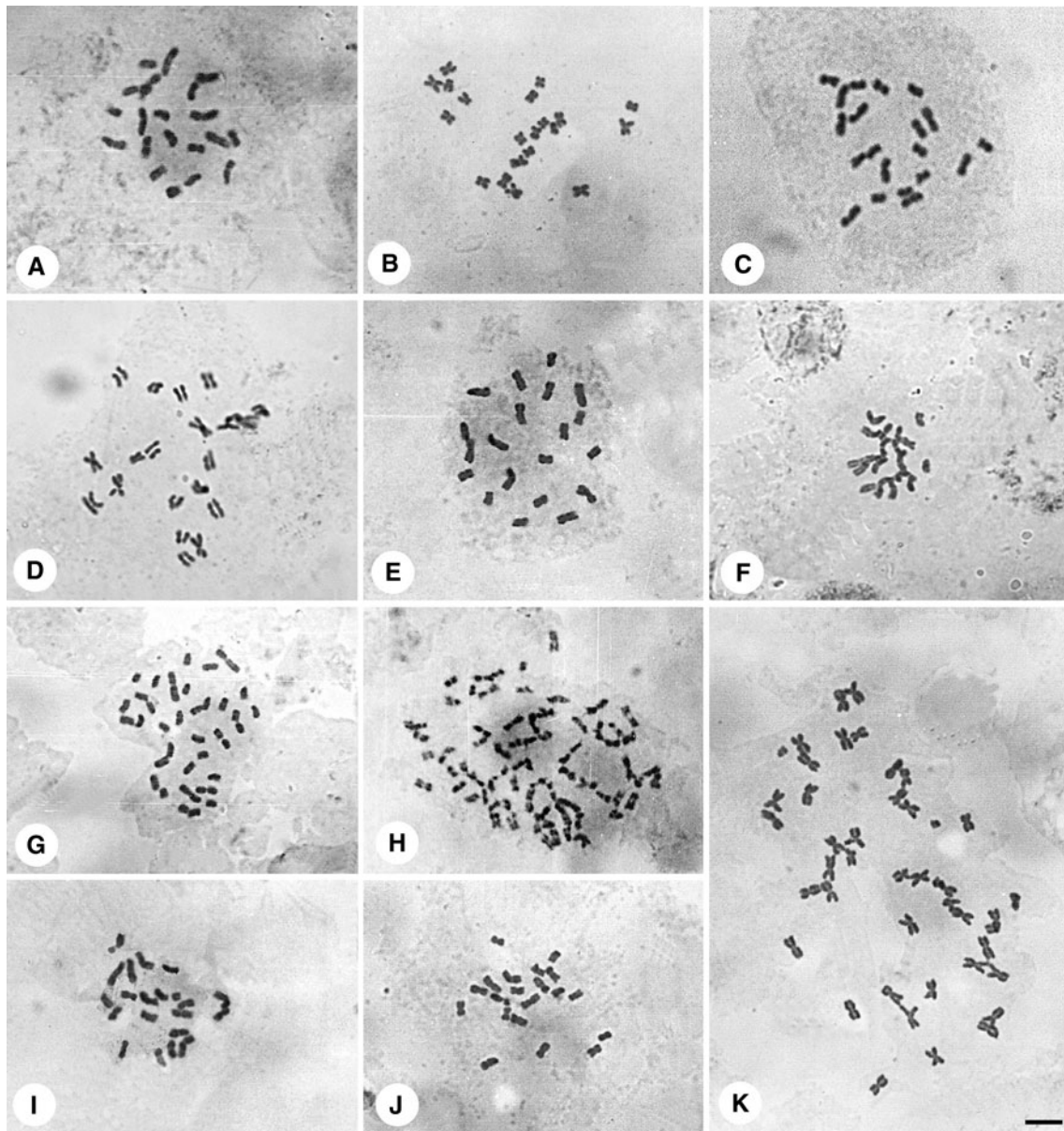
*Schizachyrium microstachyum* This species is widespread in America (Filgueiras 2003). The chromosome number  $2n = 2x = 20$  found in all the accessions from northeastern Argentina studied here confirms previous reports for plants from central Argentina (Saura 1948), Brazil, Uruguay (Gould 1956) and El Salvador (Davidse and Pohl 1974). This indicates that this widespread American species is diploid.

*Schizachyrium plumigerum* This species is endemic to South America and occurs in Argentina, Paraguay and Uruguay (Peichoto 2010). The chromosome number ( $2n = 2x = 20$ ; Fig. 1e) for accessions from Northeastern Argentina presented here is the first report for this species.

*Schizachyrium salzmännii* This species occurs in the Americas (Clayton and Renvoize 1986). In South America it grows in Argentina, Uruguay, Paraguay, southern Brazil, Bolivia, Colombia and Venezuela (Filgueiras 2003; Peichoto 2010). The diploid (Fig. 1f) and tetraploid ( $2n = 4x = 40$ ; Figs. 1g and 2c) cytotypes for this species are reported here for the first time. Both diploid and tetraploid cytotypes were found in northeastern Argentina, whereas only tetraploid cytotypes were detected in Paraguay.

*Schizachyrium sanguineum* This species is widespread in the world and occurs in Africa, America and Asia (Clayton and Renvoize 1986). It is also widespread in South America, from Colombia and Venezuela to Chile, Argentina and Uruguay (Peichoto 2010). Many chromosome counts indicating that this species is a polyploid complex have been reported from Africa (De Wet 1954; Kammacher et al. 1973; Olorode 1974; Dujardin 1978), India (Gould and Soderstrom 1974; Kalia 1978; Mehra 1982), Europe (Krupko 1953) and America (Carman and Hatch 1982; Pohl and Davidse 1971; Davidse and Pohl 1972; Norrmann et al. 1994). Although diploid cytotypes have not been found, both even and odd ploidy levels, from triploid





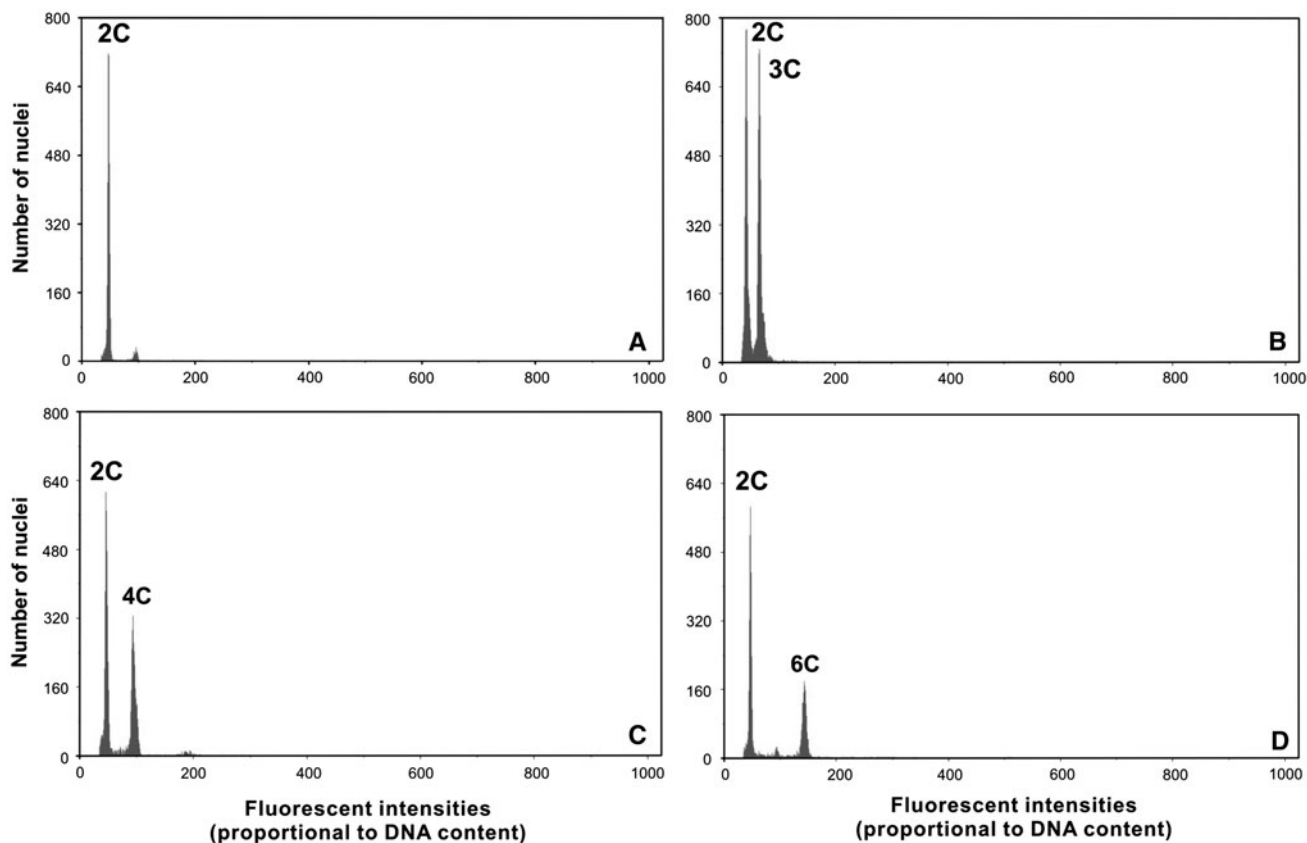
**Fig. 1** Somatic chromosomes of *Schizachyrium*. **a** *S. bimucronatum* ( $2n = 20$ ), **b** *S. glaziovii* ( $2n = 20$ ), **c** *S. gracilipes* ( $2n = 20$ ), **d** *S. lactiflorum* ( $2n = 20$ ), **e** *S. plumigerum* ( $2n = 20$ ), **f** *S. salzmannii*

( $2n = 20$ ), **g** *S. salzmannii* ( $2n = 40$ ), **h** *S. sanguineum* ( $2n = 80$ ), **i** *S. scabriflorum* ( $2n = 20$ ), **j** *S. spicatum* ( $2n = 20$ ), **k** *S. tenerum* ( $2n = 40$ ). Scale bar 5  $\mu\text{m}$

( $2n = 3x = 30$ ) to decaploid ( $2n = 10x = 100$ ), have been assigned to this species. Tetraploid ( $2n = 4x = 40$ ), pentaploid ( $2n = 5x = 50$ ) and octoploid ( $2n = 8x = 80$ ) are the most frequent and widely distributed cytotypes of this genus around the world. The main cytotype diversity was found in South America, where tetraploid, pentaploid, hexaploid ( $2n = 6x = 60$ ), heptaploid ( $2n = 7x = 70$ ) and octoploid cytotypes occur. The higher ploidy level ( $2n = 10x = 100$ ) has been reported only for populations from Southern United States (Carman and Hatch 1982). In Argentina, this species is widely distributed, although data on chromosome numbers of Argentinian populations are not

available. Our counts in accessions from Northeastern Argentina revealed the occurrence of tetraploid, pentaploid and octoploid plants (Fig. 1h).

*Schizachyrium scabriflorum* This species is endemic to South America, and has been cited for Bolivia, Paraguay, central and Southeastern Brazil and Northeastern Argentina (Filgueiras 2003; Peichoto 2010). The only previous study on chromosome number for this species found  $2n = 4x = 40$  in a Bolivian population (Killeen 1990). Our estimates in Argentinian plants are the first report of the diploid ( $2n = 2x = 20$ ) (Fig. 1i), triploid ( $2n = 3x = 30$ ),



**Fig. 2** Flow cytometric profiles of diploid and polyploid plants of *Schizachyrium*. **a** Flow cytometry histogram of a diploid plant of *S. bimucronatum* and the internal standard (P 60) with a high peak at 2C. **b** Flow cytometry histogram of a triploid individual of *S. elongatum* showing a peak at 3C and the standard P 60 (2C).

hexaploid (Fig. 2d), and octoploid ( $2n = 8x = 80$ ) levels for this taxon.

*Schizachyrium spicatum* (Spreng.) Herter This species is endemic to South America, and occurs in Argentina, Uruguay and Southern Paraguay and Brazil (Filgueiras 2003; Peichoto 2010). Ploidy level estimates for Argentinian accessions revealed that this species is diploid ( $2n = 2x = 20$ ; Fig. 1j) and this is the first report for this taxon.

*Schizachyrium tenerum* Nees This is an American species, widely distributed in South America (Clayton and Renvoize 1986; Peichoto 2010). A new chromosome number,  $2n = 4x = 40$  (Fig. 1k), is presented here for this species. Additionally, in agreement with a previous report on material from Southern United States (Gould 1956), we also report  $2n = 6x = 60$ .

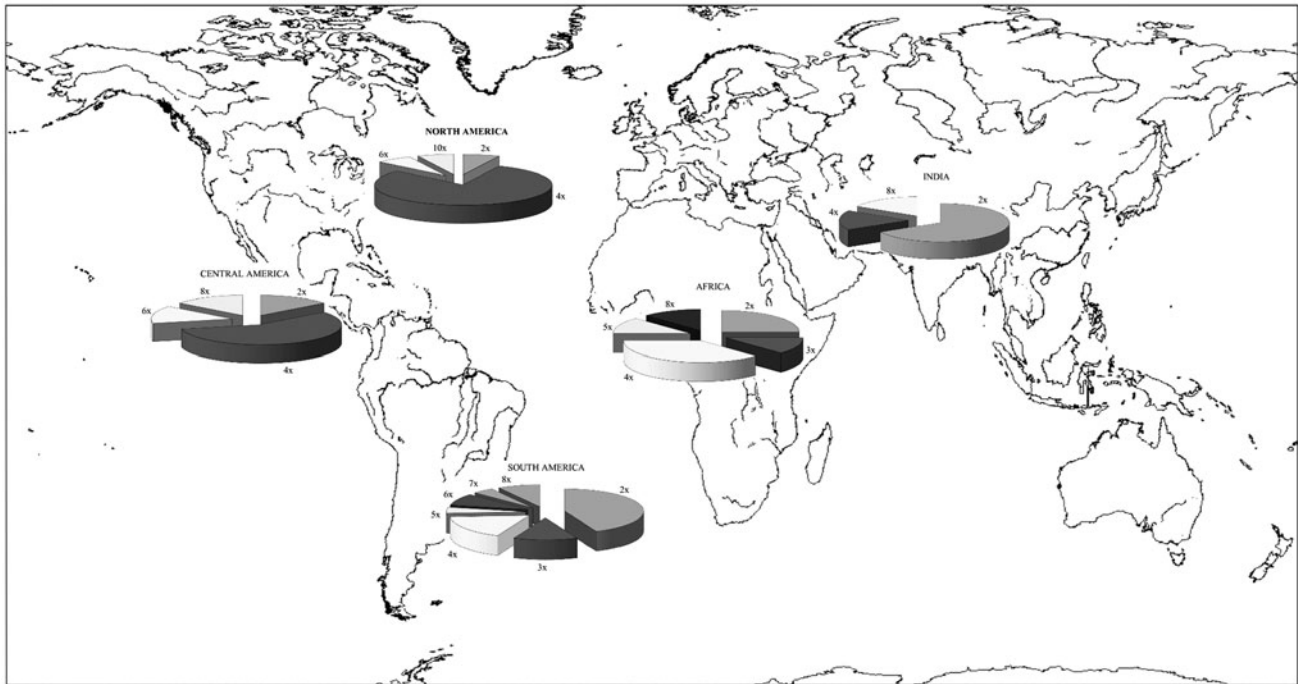
### Incidence of polyploidy

Polyploidy is a conspicuous feature of chromosomal evolution in higher plants. As many as 70–80% of

**c** Flow cytometry histogram of a tetraploid plant of *S. salzmannii* with a high peak at 4C and the diploid standard P 60 (2C). **d** Flow cytometry histogram of a hexaploid plant of *S. scabriflorum* with a peak at 6C and the standard P 60 (2C)

Angiosperms species and up to 95% of Pteridophytes have a polyploid origin (Masterson 1994; Soltis and Soltis 1999; Bennett 2004). Most Gramineae, one of the largest families of flowering plants, including approximately 10,000 species, are polyploids (Levy and Feldman 2002).

The data presented here, together with published chromosome numbers (Church 1936, 1940; Saura 1948; Brown 1950, 1951; Krupko 1953; Snyder 1953; De Wet 1954; Darlington and Wylie 1955; Tateoka 1955; Gould 1956, 1968; Carnahan and Hill 1961; Federov 1969; Pohl and Davidse 1971; Davidse and Pohl 1972; Moore 1973, 1974, 1977; Kammacher et al. 1973; Gould and Soderstrom 1974; Mehra and Kalia 1974; Olorode 1974; Dujardin and Bryne 1975; Kalia 1978; Dujardin 1978, 1979; Goldblatt 1981, 1984, 1985, 1988; Carman and Hatch 1982; Mehra 1982; Christopher and Samraj 1985; Bruner 1987; Spies and Du Plessis 1987; Goldblatt and Johnson 1990; Killeen 1990; Norrmann et al. 1994), reveal that polyploidy has played an important role in the evolution of *Schizachyrium*, since 66% of the species analyzed are polyploids. This percentage is close to the estimate that 70% of Gramineae (Stebbins 1956) are polyploids. The general occurrence of polyploidy



**Fig. 3** Percentage of polyploids of *Schizachyrium* in the different continents

in the tribe Andropogoneae is also well known. Tetraploids are about as numerous as diploids, although triploids, pentaploids, hexaploids, octoploids to 18-ploids occur in some groups (Gould 1956; Norrmann 1999; Scrivanti et al. 2010).

Although diploids and polyploids of *Schizachyrium* are distributed throughout the world, the frequency of polyploids is higher in Africa, North America and Central America, tetraploids being the most common cytotype. Moreover, in the northern hemisphere only polyploids even occur, while in the southern hemisphere odd polyploids have also been found (Fig. 3). Triploids and pentaploids have been found in Africa, and triploids, pentaploids and heptaploids in South America. The main cytotype diversity was also detected in the southern hemisphere. Up to five and up to seven different cytotypes have been found in Africa and South America, respectively.

Despite the presence of high cytotype diversity, diploid is the most frequent cytotype in South America. It was found in endemic species such as *S. bimucronatum*, *S. gracilipes*, *S. lactiflorum*, *S. plumigerum* and *S. spicatum*. This finding is in disagreement with the ploidy level found in endemic species from North America including *S. maritimum*, *S. niveum*, *S. sericatum*, as well as with that found in the varieties of *S. scoparium* (Church 1936, 1940; Brown 1951; Gould 1956, 1968; Carman and Hatch 1982; Bruner 1987), and in African species, such as *S. exile* and *S. rupestre* (Kammacher et al. 1973; Olorode 1974), which are all tetraploids.

Our results also reveal intraspecific polyploidy in some (33%) widespread South American species. Diploid and

tetraploid populations were detected in *S. salzmanii*, tetraploid and hexaploid populations in *S. tenerum*, and tetraploid, pentaploid and octoploid populations in *S. sanguineum*. Although *S. scabriflorum* is an endemic species, it has diploid, triploid, hexaploid and octoploid cytotypes. Tetraploid and hexaploid are the most frequent cytotypes among these species.

The high frequency of diploid cytotypes, together with the fact that 12 out of 19 South American species of *Schizachyrium* occur in Northeastern Argentina, Paraguay, Southern Brazil and Uruguay, supports the hypothesis that this region is an important centre of variation of the genus (Peichoto 2007). In contrast, the highest frequency of polyploids in the widespread species suggests that polyploid cytotypes may have enhanced competitive ability, fitness or ecological tolerance compared to diploid cytotypes, being able to colonize new habitats and expand their geographical range.

### Taxonomic and evolutionary implications

The infrageneric classification of *Schizachyrium* is still an unresolved problem. Roberty (1960), in his treatment of the Andropogoneae, recognized 13 species for the whole world, which were assigned to eight sections. In his review, many taxa, which are currently treated as different taxonomic entities, were considered as infraspecific categories. Taking into account that the number of the currently recognized



species does not coincide with that included in the classification of Roberty (1960) and that sections were established based only upon spikelet traits, this infrageneric classification was not adopted in further taxonomic treatments of the genus (Clayton and Renvoize 1986; Türpe 1984).

Lately, some regional taxonomic studies have been carried out in the genus *Schizachyrium* (Hatch 1975; Bruner 1987; Gandhi 1989; Peichoto 2007, 2010). As a result of a deep exomorphological analysis performed in South American species (Peichoto 2007), the species were divided into two groups. One of group contains species with highly branched feathery inflorescences and slender rachis internodes, and the other group species with sparsely branched inflorescences and thick rachis internodes. According to the criteria of Renvoize and Clayton (1992), the former inflorescence traits are considered ancestral characters and the latter are derived traits.

Some taxonomic implications can be drawn from the current analysis since the ploidy levels presented here agree with the division of the genus into two groups as proposed by Peichoto (2007). Our results show that all the species with highly branched feathery inflorescences and slender rachis internodes are mostly diploid. We can assume that during the diversification of this group of South American species changes have occurred at a morphological level, without variations of the ploidy level. On the other hand, it appears that polyploidy has played a fundamental role in the evolution of the species with advanced inflorescence traits, such as *S. salzmanni*, *S. scabriflorum*, *S. sanguineum* and *S. tenerum*, since they are mostly polyploid and exhibit intraspecific polyploidy.

The cytological studies together with the morphological analysis may well be the foundation to reassess the infrageneric organization of the genus *Schizachyrium*. This preliminary information resulting from the joint analysis of morphological and cytological data should be tested in future phylogenetic analyses in order to clarify the evolutionary lineages in the genus *Schizachyrium*.

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