FURTHER MEIOTIC STUDIES IN BRAZILIAN AND PARAGUAYAN GERMPLASM ACCESSIONS OF *Paspalum L.* (GRAMINEAE)

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1. ABSTRACT

Apomixis is frequent in the genus *Paspalum*. Possibilities of manipulation of apomixis for genetic breeding depend on a good understanding of the whole biological process involved. Considering that meiotic normality or disturbances would reflect the reproductive systems of each accession, the objective of this investigation has been to study the meiotic chromosome behavior of thirty accessions of some Brazilian species and two accessions of Paraguayan species of *Paspalum* available as germplasm. The chromosome number detected for the majority of the accessions analysed is 2n=4x=40. Three accessions of *P. almum* (2n=4x=24), two of *P. conspersum* (2n=6x=60) and one of *P. paniculatum* (2n=2x=20) were exceptions. Most of the accessions were characterized by essentially irregular meiosis at the tetraploid level. This research confirms the high frequency of polyploidy among the *Paspalum* species considered. The results show a variable number of multivalent chromosome associations, corroborating the idea that both autoploidy and alloploidy may be involved in the origin of the Brazilian and Paraguayan tetraploid accessions of *Paspalum* investigated.

Key words: *Chromosome number, chromosome pairing, forage grasses, ploidy level.*

2. INTRODUCTION

Apomixis is frequent in the genus *Paspalum*. In many of its species, it is the main mode of reproduction. Possibilities of manipulation of apomixis for genetic breeding depend on a good understanding of the whole biological process involved. This has been a problem, and as a result *Paspalum* germplasm with a forage potential has been under utilized in breeding programs (Valls, 1992). In general, cultivar releases have been only based on the agronomic screening and selection of the most productive germplasm lines, usually apomictic, followed by seed increase for commercial use. An interesting exception including crosses is provided by the continuous breeding of Pensacola bahiagrass, *P. notatum* Flügge (Burton, 1990; Gates *et al.*, 2004).

Most apomictic entities of the genus *Paspalum* are part of agamic complexes, in which diploids are self-sterile and generally show regular bivalent chromosome associations at meiosis, while the related polyploids tend to show irregular chromosome pairing and segregation, as well as aposporous and pseudogamous apomixis. Not all polyploids are apomitic. Some are autogamous sexual alloploids, with regular meiotic pairing (Quarín, 1992). Autogamous sexual diploids exist in a small proportion; self-sterile

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diploids are usually much less frequent in nature than their polyploid counterparts (Pozzobon & Valls, 1997; Quarín *et al.*, 1996). Most of the *Paspalum* entities are either autogamous or apomictic, resulting in genotipic stability, because of the lack of segregation (Quarín & Normann, 1987).

Considering that meiotic normality or disturbances would reflect the reproductive systems of each accession, the objective of this investigation has been to study the meiotic chromosome behavior of some Brazilian and Paraguayan species of *Paspalum* available as germplasm. Such investigation could provide indirect evidence of the probable occurrence of apomixis in most accessions.

3. MATERIAL and METHODS

Plant material was obtained primarily from germplasm explorations in Brazil. Two accessions have been collected in Paraguay. All the accessions analyzed are part of the *Paspalum* germplasm collection at EMBRAPA (Empresa Brasileira de Pesquisa em Agropecuária), Embrapa Recursos Genéticos e Biotecnologia (CENARGEN), Brasília, DF, Brazil. Original voucher specimens are deposited in the CENARGEN Herbarium (CEN), Brasília, Brazil. **Table 1** lists the species and accessions studied and their collection sites.

For meiotic analysis, young inflorescences were fixed in 3:1 solution of absolute ethanol: glacial acetic acid for 24h, and stored in 70% ethanol at 5°C until required. Slides were prepared by squashing the anthers in 2% propionic carmine. To analyze chromosome pairing, the highest available number of well-spread cells at diakinesis and metaphase were examined. Besides, to follow all the meiotic process, all available and well-spread cells in other meiotic phases were examined. Meiotic chromosome preparations were observed with light transmission microscopy and the results were recorded by photomicrographs.

4. RESULTS and DISCUSSION

The results of the cytogenetic analysis, with cytological configurations at diakinesis and metaphase I in PMCs are summarized in **Table 2 (Anexo1)**. The chromosome number detected for the majority of the accessions analyzed is 2n=40. Most of the accessions were characterized by essentially irregular meiosis at this ploidy level. Except for the three *P. almum* Chase accessions (2n=24), all diploid, tetraploid or hexaploid species and accessions showed a basic number x=10.

Paspalum almum is peculiar in the genus, due to its 2n=4x=24 chromosomes, confirmed in populations from Texas, Argentina and Brazil (Burton, 1942; Fernandes *et al.*, 1974; Burson, 1975; Quarín, 1974; Pozzobon & Valls,1987; Honfi *et al.* 1990). Based on this distinct somatic number, a new basic number has been proposed for *Paspalum*. Burton (1942) suggested x=6 or 12, while Fernandes *et al.* (1974) proposed x=6, possibly deriving from x=5. The finding of 2n=12 in *P. hexastachyum* (Quarín, 1974), which should be considered conspecific with *P. almum* (Valls, 2000; Zuloaga *et al.*, 2003), eliminates the possibility of x=12. The reproduction of tetraploid *P. almum* by aposporic apomixis and its characterization as an autotetraploid species, showing sometimes 5 IV, supports the hypothesis of a base number of six (Burson, 1975) possibly derived from x=5 (Quarín & Hanna, 1980b). In this analysis, *P. almum* has shown varying numbers of univalents, bivalents, trivalents and quadrivalents during diakinesis and metaphase I (**Figure 1A and B**). As many as three quadrivalents were observed. Bridges and laggards were observed in telophase I. Meiosis II was irregular, with presence of asynchronic divisions, laggards and micronuclei.

Paspalum conspersum Schrader has been characterized as an hexaploid, with regular meiotic behavior (Quarín & Hanna, 1980a; Pozzobon & Valls, 1987; Pagliarini *et al.*, 2001), sexual reproduction and allopolyploid origin (Quarín & Hanna, 1980a). Our new re-

Table 1. *Paspalum* species and accessions investigated.

Species	Accession Code (BRA-)	Collector number[1]	Site of origin[2,3]
P. almum Chase	017159	V 12326	BRA, RS, Dom Pedrito
	017558	V 12396	BRA, RS, Uruguaiana
	017566	V 12397	BRA, RS, Uruguaiana
P. atratum Swallen	018996	Ry s/nº	BRA, MS, Campo Grande
P. conspersum Schrader	008354	V 9407	BRA, MT, S. Ant. do Leverger
	012467	V 11726	BRA, MS, Paranaiba
P. guenoarum Arech.	004880	V 8020	BRA, SC, São Joaquim
	003824	V 8563	BRA, MS, Bela Vista
P. maculosum Trinius	011240	V 10714	BRA, RS, Cruz Alta
P. paniculatum L.	002658	V 5092	BRA, GO, Itumbiara
P. plicatulum Michaux	009211	EEA 148	BRA, RS, Eldorado do Sul
	009229	EEA 149	BRA, RS, Eldorado do Sul
	008893	V 4331	BRA, RS, São Gabriel
	003450	V 7441	BRA, SC, Lages
P. regnellii Mez	012947	V 11900	BRA, MS, Aral Moreira
P. (Plicatula group) sp.	022501	As 293	BRA, MG, Patrocínio
	008699	D 163	BRA, SC, Lages
	010235	Sv 536	BRA, MG, Montes Claros
	009083	V 4741	BRA, RS, São Sepé
	009105*	V 4793	BRA, RS. Guaíba
	010642	V 7333-A	BRA, RS, Itaqui
	009547	V 9414	BRA, MT, S. Ant. do Leverger
	009601	V 9474	BRA, MS, Aquidauana
	009628	V 9884	BRA, MS, Anastácio
	009661	V 9908	BRA, MS, Aquidauana
	009687	V 9922	PRY, Bella Vista
	009695	V 9927	PRY, Bella Vista
	010596	V 10503	BRA, MT, N. S^{ra} do Livramento
	-	V 10504	BRA, MT, N. S^{ra} do Livramento
	012980	V 11912	BRA, MS, Amambai
P. virgatum L.	012734	V 11830	BRA, MS, Caarapó
	012785	V 11844	BRA, MS, Navirai

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[2] Brazilian States: GO: Goiás; MG: Minas Gerais; MS: Mato Grosso do Sul; MT: Mato Grosso; RS: Rio Grande do Sul; SC: Santa Catarina

[3] Countries: BRA: Brazil; PRY: Paraguay

* Cited as *P. compressifolium* by Adamowski *et al.* (2005).

sults confirm these data (2n=60) for two additional accessions. Meiosis was quite regular, with the chromosomes pairing primarily as 30 II (**Figure 1C**). Anaphase and telophase I were considered regular. Several accessions from Brazil have been wrongly cited as sexual tetraploids of *P. conspersum* (Fernandes *et al.*, 1974; Burson and Bennett, 1976; Burson, 1978). However these accessions where misidentified specimens of *P. regnellii* Mez, identified on the basis of voucher specimens available.

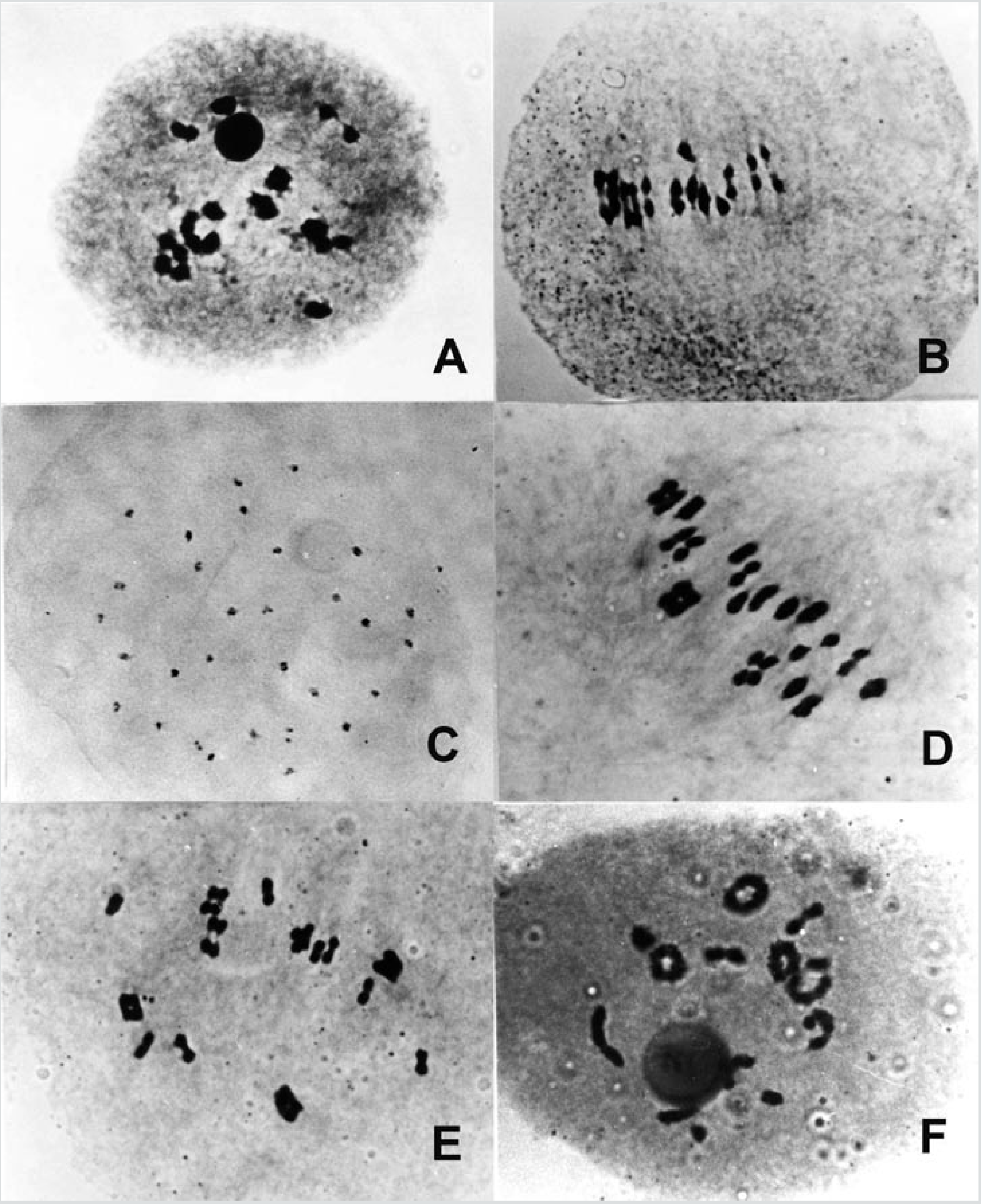

Figure 1. *Paspalum almum*: A) Late diakinesis with 8II + 2IV; B) Metaphase I with 8II + 2IV (1II with early desynapsis). C) *P. conspersum*, diakinesis showing 30II. D) *P. plicatulum*, metaphase I with 14II + 3IV. E) *P.* (Plicatula group) sp., metaphase with 8II + 6IV. F) *P. guenoarum*, diakinesis showing 2I + 7II + 6IV.

All accessions of *Paspalum* in the Plicatula group, including those of *P. atratum* Swallen, *P. guenoarum* Arech., *P. plicatulum* Michaux and others with their taxonomic circumscription not yet defined, presented 2n=40 chromosomes. Although irregular, their meiosis showed mainly bivalents and quadrivalents in diakinesis and metaphase I (**Figure 2C**). Unbalanced chromosome segregation at anaphase I (**Figure 2B**) and micronuclei were present in telophase I cells, and we observed similar irregularities at anaphase and telophase II (**Figure 2G**). Bridges and laggards also were observed, as well as asynchronic divisions. Irregular meiotic behavior prevails in this group, as well as in other apomitic tetraploids of *Paspalum*.

Meiotic chromosome behavior in *P. atratum* showed a broader range of associations than those reported by Quarín *et al.* (1997) for a different accession of the species. The same authors reported this species to be apomictic, with aposporous embryo sac formation followed by parthenogenesis, and with an exceptionally good seed set for an apomitic *Paspalum*. The accession studied here does produce seed and shows a more irregular meiosis, which seems to indicate a similar apomictic reproduction.

Paspalum plicatulum is cited as tetraploid and apomictic (Bashaw *et al.*, 1970; Pritchard, 1970; Burson & Bennett, 1971b) and usually behaves as a segmental allotetraploid. The occurrence of rare diploids has been recorded for the species (Brown, 1950; Reeder, 1967; Davidse & Pohl, 1972; 1978; Fernandes *et al.*, 1974; Honfi *et al.*, 1990; Pozzobon *et al.*, 2000). Sexuality at the diploid level has been confirmed by Espinoza & Quarín (1997). *Paspalum guenoarum* is an apomitic tetraploid (Pritchard, 1970), considered to be of segmental allotetraploid origin (Burson & Bennet, 1971a). Additional Brazilian accessions of *P. plicatulum* and *P. guenoarum* were previously analyzed by Fernandes *et al.* (1974) and Pozzobon & Valls (1987). Their meiotic behavior is similar to that of accessions cited in this paper. The presence of associations involving five or more chromosomes besides quadrivalents (**Figures 1D to F and 2A**) suggests that autopolyploidy may have been important in the origin of these species.

Additional Brazilian accessions of the last three species above were analized by Takayama *et al.* (1998), all showing the tetraploid level. The meiotic behavior of four of the accessions counted by Takayama *et al.* (1998) (EEA 148, V 4331, V 9884) is analyzed here.

Most of the accessions still without a species name in the Plicatula group exhibited very limited trivalent pairing. A higher average frequency of univalents in relation to trivalents is acceptable in polyploids of an even level, because the univalents can originate from early desynapsis or failure in the formation of quadrivalent (III+I) and bivalents (I+I). The higher number of bivalents as compared to quadrivalents and univalents, and lastly to trivalents or other associations, is constant (**Figure 3F**).

Some accessions (V 4793, V 9414, V 9908 and V 9922), showed a high frequency of univalents (**Figures 2E and F**), emphasizing a lack of pairing that could be due to partial asynapsis. The presence of multiple nucleoli is common in the accessions analyzed (**Figure 2D**). The presence of multiple nucleoli in diakinesis of several *Paspalum* species has been recorded by Sacchet (1973) and in *P. plicatulum* by Nath *et al.* (1970).

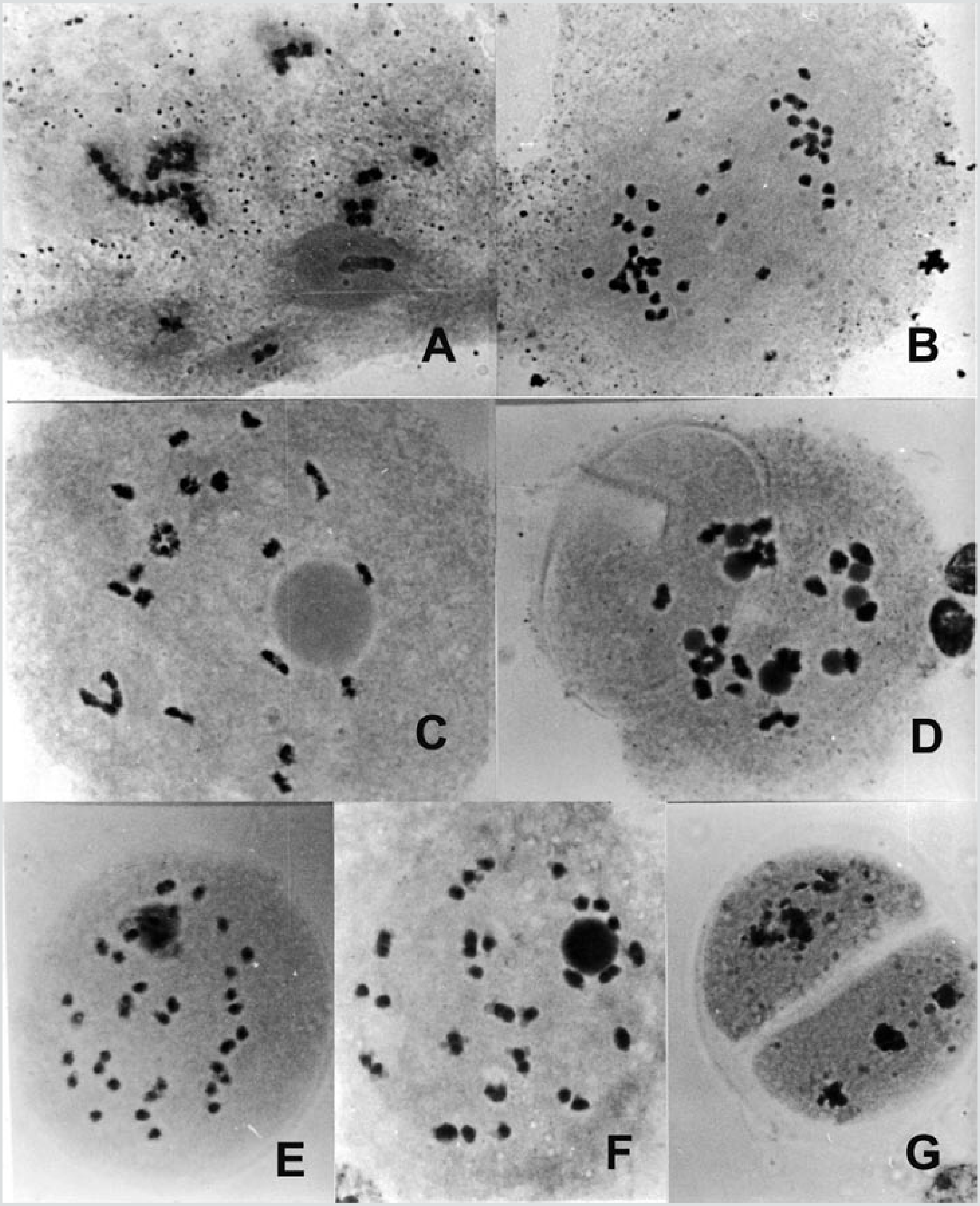

Figure 2. *Paspalum guenoarum*: A) diakinesis showing 5II + 4IV + 1VI + 1VIII; B) Unbalanced segregation at anaphase I with 15 chromosomes at one pole (top), 20 at the other (bottom), and five laggards. *Paspalum* (Plicatula group) *sp*: C) V 7333-A, diakinesis with 16II + 2IV; D) V 10503, diakinesis with 1I + 12II + 1III + 3IV and multiple nucleoli; E) V 9908, diakinesis with 28I + 6II; F) V 9908, diakinesis with 16I + 12II; G) V 9908, telophase II showing unbalanced chromosome segregation.

Paspalum paniculatum L. had 2n=2x=20 chromosomes predominantly pairing as bivalents (**Figure 3E**). Univalents were present at metaphase I and laggards were occasionally observed in telophase I. Diploidy is already cited for Brazilian and Argentinean accessions of this species (Fernandes *et al.*, 1974; Honfi *et al.*, 1990). However, Honfi *et al.* (1990) also found one tetraploid accession of the species, among Argentinean materials.

Paspalum regnellii showed 2n=40 chromosomes, which were characterized by normal pairing, with a predominance of cells with bivalents at diakinesis and metaphase I. The chromosome number is in agreement with previous evaluations carried out by Norrmann (1981) and Honfi *et al.* (1990). According to Norrmann (1981), this species reproduces sexually and is of allotetraploid origin.

Norrmann *et al.* (1989) and Pozzobon *et al.* (2000) reported 2n=40 for brazilian accession of *P. maculosum* Trinius. The accession here studied is also tetraploid and averaged a smaller number of quadrivalents, which may be an artifact of the small number of cells analyzed (**Figures 3A to D**). This species has been known as a diploid with a regular behavior in meiosis (Fernandes *et al.*, 1974), characterized as sexual and self-incompatible (Norrmann *et al.*, 1989). The tetraploids were characterized as facultative apomictics (Norrmann *et al.*, 1989). The similarity of morphological characteristics of diploids and tetraploids and the presence of multivalent associations suggest that tetraploid in this species originates from autoploidy (Norrmann *et al.,* 1989).

The meiotic behavior of the two accessions of *P. virgatum* L. has been quite similar to that reported by Burson & Quarín (1982) for materials from Brasil and Colombia. The species is considered as sexual and meiotically stable and our data confirm the occasional occurrence of rare univalents and quadrivalents.

According to Quarín (1992), a substantial number of *Paspalum* species are characterized by apomictic autotetraploid races and sexually reproducing self-sterile diploid counterparts. Diploids may have an outstanding incidence in the genetic variability and evolution of apomictic tetraploid *Paspalum* species, by maintaining the contact of apomictic tetraploids with sexuality in mixed populations (Espinoza & Quarín, 1997; Daurélio *et al.*, 2004).

In most of the literature on the origin of tetraploids, definitions are based on the number and frequence of quadrivalents and other associations, besides morphological similarities. This would indicate the level of genome homology, either partially homologous, indicating segmental allopolyploidy, or homologous, suggesting autopolyploidy. Extensive evidence obtained in *Paspalum* supports the hypothesis that both autoploidy and segmental alloploidy may have been involved in the origin of apomictic tetraploids (Quarín, 1992; Quarín *et al.*, 2001). Evidence of autoploidy has been reported for some apomictic species (Quarín *et al.*, 1984; Pupilli *et al.*, 1997; Quarín *et al.*, 1998). In the present work, the results show a variable number of multivalent chromosome associations, corroborating the idea that both autoploidy and alloploidy may be involved in the origin of the Brazilian and Paraguayan tetraploid accessions of *Paspalum* investigated.

The data presented in this paper confirm the high frequency of polyploidy among the *Paspalum* species considered. This fact supports the importance of polyploidy in the evolution of tropical South American grasses and also may reflect a superior adaptability associated to the tetraploid level. The results also demonstrate that in a tetraploid species it is possible to find accessions with different degrees of meiotic irregularities. This is important to identify the best accessions for using as male progenitors in breeding programs and in the selection of promising apomictic accessions. Detailed meiotic studies should be extended to the largest possible number of accessions and species of *Paspalum* and related genera.

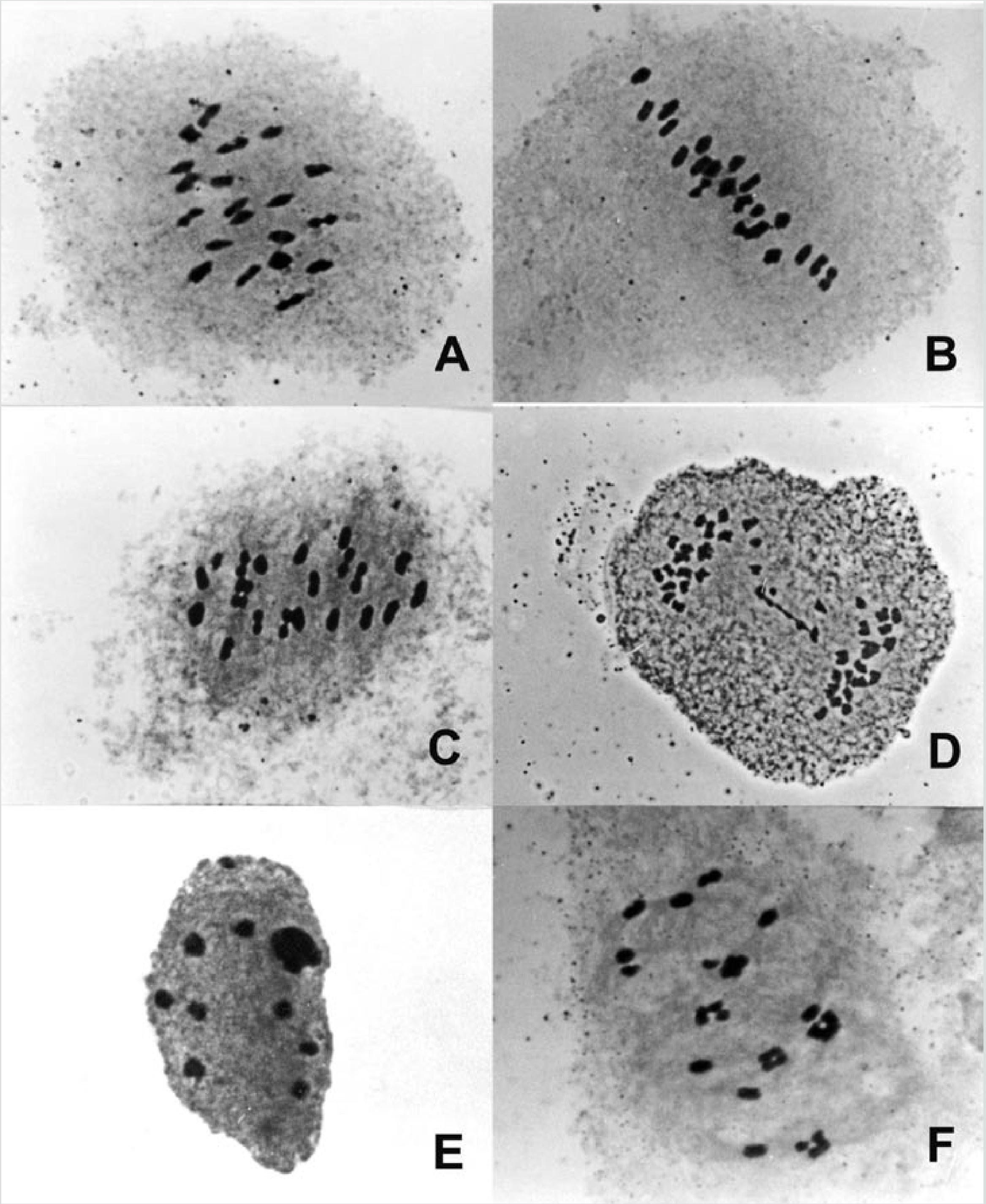

Figure 3. *Paspalum maculosum*: A) Metaphase I showing 20II, B) Metaphase I with 1I + 18II + 1III, C) Metaphase I with 16II + 2IV, D) Late anaphase I with bridge and chromosome fragments. E) *P. paniculatum*, diakinesis in with 10II. F) *Paspalum* (Plicatula group) *sp*. V 10504, metaphase I in with 2I + 9II + 5IV.

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ANEXO 1

Table 2. Meiotic chromosome associations in Brazilian and Paraguayan germplasm accessions of *Paspalum.*

Species/Accession	2n	Nº PMCs	Average/ PMC (Range in parenthesis)						
			I	II	III	IV	Other associations		
P. almum									
V 12326	24	22	1.1 (0-4)	9.4 (5-12)		1.0 (0-3)			
V 12396	24	19	0.3 (0-2)	9.4 (6-12)	0.1 (0-1)	1.1 (0-3)			
V 12397	24	28	0.1 (0-2)	10.2 (6-12)	0.9 (0-3)				
P. atratum									
Ry s/nº	40	58	1.1 (0-10)	17.5 (12-20)	0.1 (0-1)	0.9 (0-4)			
P. conspersum									
V 9407	60	35		30.0 (30)					
V 11726	60	83		30.0 (30)					
P. guenoarum									
V 8020	40	71	0.8 (0-5)	14.3 (7-20)	0.2 (0-2)	2.5 (0-6)			
V 8563	40	53	0.9 (0-4)	11.4 (4-19)	0.3 (0-2)	3.6 (1-8)	0.04V (0-1)	0.1VI (0-1)	0.02VIII (0-1)
P. maculosum									
V 10714*	40	46	0.7 (0-4)	18.7 (14-20)	0.1 (0-2)	0.4 (0-3)			
P. plicatulum									
EEA 148	40	20	1.0 (0-3)	16.2 (11-20)	0.2 (0-2)	1.5 (0-4)			
EEA 149	40	22	0.7 (0-2)	14.9 (9-20)		2.4 (0-5)			
V 4331	40	19	0.4 (0-2)	19.4 (17-20)		0.2 (0-1)			
V 7441	40	40	0.2 (0-2)	15.5 (9-20)	0.1 (0-1)	2.1 (0-5)			
P. paniculatum									
V 5092*	20	14	0.2 (0-2)	9.9 (9-10)					
P. regnellii									
V 11900	40	59		20.0 (20)					
P. virgatum									
V 11830	40	16	0.8 (0-4)	18.5 (13-20)	0.2 (0-2)	0.4 (0-1)			
V 11844	40	21		19.8 (18-20)		0.05 (0-1)			
P. (Plicatula group) sp.									
As 293	40	20	0.2 (0-2)	19.3 (18-20)	0.1 (0-1)	0.2 (0-1)			
D 163	40	22	0.5 (0-3)	13.0 (8-18)	0.2 (0-2)	3.2 (1-6)			
Sv 536*	40	52	0.6 (0-4)	15.0 (8-20)	0.2 (0 - 2)	2 .2 (0-5)			
V 4741	40	18	0.4 (0-2)	15.2 (10-19)	0.1 (0-1)	2.2 (0–5)			
V 4793	40	46	0.3 (0-2)	13.7 (6-18)	0.1 (0-1)	3.0 (1-10)			
V 7333-A	40	36	0.4 (0-4)	17.8 (14-20)	0.1 (0-1)	0.9 (0-3)			
V 9414	40	21	4.6 (0-10)	14.7 (11-19)	0.1 (0-1)	1.5 (0-3)			
V 9474	40	14	0.3 (0-2)	15.0 (10-18)		2.4 (1-5)			
V 9884	40	54	0.3 (0-2)	11.7 (4-18)	0.1 (0-2)	4.0 (1-8)			
V 9908	40	53	5.2 (0-28)	17.0 (6-20)	0.1 (0-1)	0.1 (0-1)			
V 9922	40	20	4.3 (2-10)	12.7 (9-17)	0.3 (0-2)	2.3 (1-4)			
V 9927	40	24	0.2 (0-2)	12.1 (6-17)	0.04 (0-1)	3.9 (1-7)			
V 10503	40	42	0.3 (0-2)	14.4 (6-20)	0.1 (0-1)	2.6 (0-7)		0.02 VI (0-1)	
V 10504	40	38	0.9 (0-6)	14.2 (9-18)	0.1 (0-1)	2.6 (1-5)			
V 11912	40	19	1.4 (0-4)	16.6 (13-19)	0.1 (0-1)	1.3 (0-3)			

Nº PMCs=Number of Pollen Mother Cells.
*Chromosome counts by Pozzobon *et al.* (2000)