Cytological Studies in the Tribe Paniceae, Gramineae

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Graminaceous plants have been of great interest to students of plant evolution and cytotaxonomy. The so called 'modern' criteria (Stebbins and Crampton 1961), viz., chromosome numbers and their behaviour during meiosis (Stebbins 1956 a, b), embryo structure (Reeder 1957, 1961, 1962), persistent nucleoli (Brown and Emery 1957), leaf anatomy (Brown 1958), physiology (Al-Aish and Brown 1958), geographical distribution (Hartley 1958), protein characteristics (Hall 1959, Johnson and Hall 1965), the first seedling leaf (Kuwabara 1960), character association analysis (Mehra and Anderson 1961), reserve carbohydrates (Tateoka 1962), lodicule, style base and lemma (Hsu 1965) and, essential oils (de Wet and Scott 1965) etc., have been found useful in characterizing the major taxa within the family. All these criteria taken together help to understand the origin and interrelationships of different taxa.

Cytological studies were initiated on several grasses of economic interest in the Division of Botany of the Indian Agricultural Research Institute, New Delhi in 1954 (see review of Jauhar and Joshi 1961 c). These studies revealed the occurrence of intra-specific chromosome races in several genera of the tribe *Andropogoneae* (Mehra 1954, 1955 a, b, Mehra *et al.* 1962) and *Paniceae* (Nath and Swaminathan 1957, Joshi *et al.* 1959, Patil *et al.* 1962), new basic chromosome numbers in genus *Pennisetum* (Swaminathan and Nath 1956 a, Joshi *et al.* 1959) and the presence of B-chromosomes in *Panicum coloratum* L. (Swaminathan and Nath 1965 b), *Chrysopogon gryllus* (Linn.) Trin. (Mehra *et al.* 1962), *Panicum nehruense* Jauhar et Joshi (Jauhar and Joshi 1966 c) and *Panicum maximum* (Jauhar 1967). This paper deals with the cytological studies conducted in 8 genera of the tribe Paniceae, Gramineae.

Material and methods

Several grass species obtained from various sources were grown in the Botany and Agronomy Divisions of the India Agricultural Research Institute.

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Plants were cut at different times to increase the flowering duration.

Bud materials employed for microsporogenesis were fixed between 9 to 12 A.M. in propionic-alcohol (1:3) saturated with ferric-acetate. Propionocarmine smears were prepared according to Swaminathan *et al.* (1954). Occasionally, materials fixed in Carnoy's solution (1:3:6) gave better results than those fixed in propionic-alcohol. The slides were made permanent according to the schedule of Bhaduri and Ghosh (1954). Pollen fertility was studied as stainability in acetocarmine.

Observations and discussions

The tribe Paniceae, one of the largest tribes of the grass family, consists of 81 genera (s.str., Potztal 1956) and more than 1300 species (Prat 1960, recognized only 41 genera). In this study, 8 genera were analyzed cytologically.

Brachiaria Griseb

This genus consists of about 80 species distributed in the warm regions of both hemispheres, mostly in Africa. Many species are important constituents of grasslands in warm areas of high rainfall. *Brachiaria* differs from the other genera in its strictly racemose inflorescences and the abaxial position of the spikelet. The abaxial upper glumes and the papillose-rugose upper florets are its additional distinct features.

B. brizantha (Hochst. ex. A. Rich.) Stapf

The entry studied showed 36 somatic chromosomes. Counts of $2n=18$ (de Wet 1960), 36 (Nath and Swaminathan 1957, de Wet 1960, Tateoka 1965 a, 1965 b) and 54 (Moffett and Hurcombe 1949) have been recorded for the species. It suggests the presence of intraspecific polyploidy. The taxonomic status of these chromosome races is unknown.

Because of the extreme stickiness of the chromosomes, well spread diakinesis and metaphase I stages could not be secured in enough pollen mother cells to analyze the average frequencies of the chromosome configurations. Several univalents were, however, observed both at diakinesis and metaphase I. In one cell, 12 bivalents and 12 univalents were clearly observed. Lagging chromosomes and irregular distribution of chromosomes to the poles were observed at anaphase I (Fig. 1). One cell showed a maximum of 18 lagging chromosomes. The nuclear masses formed at the end of the first division were, in most cells, linked by a chromatic bridge. It suggests that the extreme stickiness of chromosomes observed at the earlier stages prevents the complete separation of the two daughter nuclei (Fig. 2). Double restitution nuclei with 72 chromosomes were occasionally observed. Pollen fertility, perhaps as a result of the pronounced meiotic irregularities, was only 20 per cent. Seed set was less than 1 per cent.

B. decumbens Stapf

This species is distributed in tropical Africa. The entry studied had 36

somatic chromosomes. This count agrees with that of Zerpa (1952). Several cells at diakinesis (Fig. 3) and metaphase I showed varying numbers of univalents (2-6) and bivalents (15-17). Mean chiasma frequencies per bivalent were 1.9 and 1.8 at diakinesis and metaphase I, respectively. At anaphase and telophase I, 1 to 7 lagging chromosomes were observed in 74 per cent of the cells. Pollen fertility and seed set were 24 and 1 per cent, respectively.

B. lata (Schumacher) C. E. Hubb.

This species is distributed in west tropical Africa. An entry from Sudan had 48 somatic chromosomes. Its meiotic behaviour was regular. Twenty-four bivalents were counted in several cells at diakinesis and metaphase I (Fig. 4). The bivalents were of variable size, 2 large, 17 medium and 5 small. Mean chiasma frequencies per bivalent at diakinesis and metaphase I were 1.99 and 1.85, respectively. Chromosome disjunction at anaphase I was mostly regular. Rarely one or two lagging chromosomes were seen at this stage. Pollen fertility and seed set were 96 and 94 per cent, respectively. At present, it is not possible to speculate on the origin and taxonomic status of $2n=48$ strain of *B. lata*. Collections of this species from different areas of its geographic distribution need to be studied cytologically.

B. mutica (Forssk) Stapf

An Australian entry of this species had 36 somatic chromosomes. Hunter (1934) and Burton (1942) also reported $2n=36$ for this species. The meiotic behaviour was fairly regular. Eighteen bivalents were counted at both diakinesis and metaphase I (Fig. 5). Chiasma frequencies per bivalent at diakinesis and metaphase I were 1.9 (average of 30 cells) and 1.68 (average of 44 cells), respectively. A few cells had unequal nucleoli at diakinesis. Their origin may be due to the cleavage of the single nucleus. In a few cells, a large number of unequal sized nucleolar bodies (as many as 8 in some cells) were observed at diakinesis. Pollen fertility was 80 per cent. The seed set was nil.

Cenchrus Linn.

This genus composed of 25 species is distributed in the warmer parts of both hemispheres.

In this genus, spikelets are subtended by a spiny bur and are arranged on the main axis to form a simple terminal raceme. The bristles or spines of the involucre are united at least near the basal part. This is a well differentiated genus closely related to *Pennisetum*. Both of them have horizontally elongated depressions in the upper florets. In *Pennisetum*, the transverse ridges are usually replaced by a silica-cell, and are not thickly convex (convex in the genus *Cenchrus*).

C. ciliaris Linn.

This species is distributed in hotter and drier parts of India, Pakistan,

Figs. 1-10. Meiosis in Paniceae (Magnification 1065 $\times$). 1, anaphase I in *Brachiaria brizantha* showing lagging chromosomes. 2, dyad cells in *Brachiaria brizantha* showing persistent sticky chromosome bridges. 3, diakinesis in *Brachiaria decumbens* showing 18 bivalents. 4, diakinesis in *Brachiaria lata* showing 24 bivalents. 5, metaphase I in *Brachiaria mutica* showing 18 bivalents. 6, diakinesis in *Cenchrus ciliaris* showing I trivalent, 13 bivalents and 6 univalents. 7, metaphase I in *Cenchrus ciliaris* showing 2 quadrivalents, 13 bivalents and 2 univalents. 8, anaphase I *Cenchrus ciliaris* showing a

the Mediterranean region, and tropical and south Africa. It grows in dry sandy and stony soils, often on hillsides. This species commonly called 'Blue Buffalo Grass' is hardy and drought resistant and is very valuable as a fodder grass.

Present study was conducted in 6 accessions, three from India (Karnal, Hissar and Delhi) and one each from Ceylon, Australia and U.S.A. Their chromosome numbers were $2n=36$ (Karnal, Hissar and Delhi accessions), 44 (Ceylon and Australia) and 52 (U.S.A.), respectively. Somatic chromosome numbers reported for this species are 32 (Krishnaswamy 1940, Delisle 1963), 34 (Pienaar 1955, Gould 1956, Delisle 1963) 35 (Delisle 1963), 36 (Krishnaswamy 1940, de Wet and Anderson 1956, Gould 1958, Delisle 1963) 40 and 43 (Delisle 1963), 44 (Nath and Swaminathan 1957, Delisle 1963), 54 (Fischer *et al.* 1954, Delisle 1963), 56 (Ponnaiya *et al.* 1966) and 78 (Gould 1965). The species, therefore, contains chromosome races.

Meiosis was irregular and the accessions differed in the frequency of various chromosomal irregularities. Multivalents and univalents were observed in all accessions at diakinesis and metaphase I (Fig. 6 and 7, Table 1). In one cell, six quadrivalents were observed at diakinesis in the strain from Hissar. The mean chiasma frequency per cell at metaphase I in these strains ranged from 23.50 to 42.50 (Table 1). Both ring and rod type bivalents were observed. At anaphase I, irregular distribution of chromosomes, chromosome bridges with fragments and both dividing and non-dividing lagging univalents were observed in all accessions but their relative frequencies differed (Fig. 8, 9 and 10). About 30 to 40 per cent of the cells showed no lagging chromosomes. The second meiotic division in the two daughter cells was non-synchronized. Lagging chromosomes were encountered in several cells at anaphase II. Lagging chromosomes (6-19) formed micronuclei at the end of the second division. A maximum of 25 micronuclei were observed in the strain from U.S.A. Pentads, hexads, heptads 9-ads etc., were observed besides normal tetrads. Pollen fertility was low in most of the accessions, but seed set ranged from 10-40 per cent.

The phenotypic uniformity of the progenies raised from the seed of these accessions suggests that the chromosomal irregularities found in the intraspecific chromosome races are associated with an apomictic mode of reproduction. Apomixis and polyembryony have already been reported in this species (Fischer *et al.* 1954, Snyder *et al.* 1955, Bashaw 1962). The occurrence of 6 (out of possible 9) quadrivalents in the strain from Hissar suggests that this collection may be an autopolyploid. Typical autopolyploid plants appear to be rare in nature, except in apomicts. Aneuploidy in the species could have arisen through chromosome deletion. Also, the factors favoring the accumulation of chromosome structural changes are in operation

chromosome bridge and a fragment. 9, anaphase I in *Cenchrus ciliaris* showing 44 chromosomes in the strain from Ceylon. 10, anaphase I in *Cenchrus ciliaris* showing irregular distribution of chromosomes to the two poles.

in the species. The evolutionary significance and the taxonomic status of chromosome races of this species is not yet clear. Natural selection, however, appears to favor their establishment through apomixis.

Table 1. Chromosome associations and chiasma frequencies at diakinesis and metaphase I in some species of Paniceae. Meiotic stages: D=Diakinesis, M=Metaphase I; Chromosome association, I, II, III and IV represent univalents, bivalents, trivalents and quadrivalents respectively. R and M denote range and mean per cell, respectively

Material	Location	Meiotic stage	Chromosome association								Mean no. chias- mata per cell
			I		II		III		IV		
			R	M	R	M	R	M	R	M	
<i>Cenchrus ciliaris</i>	1. Delhi, India	M	0-1	0.25	14-18	16.00	0-1	0.25	0-1	0.75	29.75
	2. Hissar, India	M	2-6	0.60	5-16	14.90	—	—	0-6	1.40	32.40
	3. Karnal, India	M	0-11	3.05	10-18	14.95	0-2	0.67	0-2	0.26	23.50
	4. Australia	M	3-7	5.50	17-18	17.75	0-1	1.00	—	—	32.50
	5. Ceylon	M	3-7	5.30	14-18	16.00	0-2	0.90	0-4	1.00	31.23
	6. U.S.A.	M	7-10	7.17	15-25	20.40	0-2	0.40	0-4	1.20	42.50
<i>Panicum maximum</i>	1. Delhi	D	0-1	0.20	8-16	13.41	0-1	0.06	0-4	1.20	30.83
	India	M	0-4	0.40	10-16	15.60	—	—	0-1	0.10	28.60
	2. Coimbatore	D	0-2	0.30	8-16	14.20	0-1	0.10	0-2	0.75	28.00
	India										
	3. Ajmer	D	0-1	0.20	7-16	12.10	0-2	0.40	0-3	1.60	30.40
	India	M	0-1	0.25	7-16	13.00	0-2	0.25	0-3	1.25	27.40
	4. Australia	D	—	—	12-16	15.20	—	—	0-2	0.40	31.65
		M	0-2	0.40	10-16	15.20	—	—	0-1	0.30	28.70
5. Brazil	D	—	—	4-14	13.50	—	—	0-2	1.25	26.95	
	M	—	—	6-15	14.00	—	—	0-2	1.00	26.80	
<i>Paspalum orbiculare</i>	Palampur, India	D	0-8	4.00	23-27	25.00	—	—	—	—	45.90
		M	2-12	7.50	21-25	23.25	—	—	—	—	43.50
<i>Paspalum plicatulum</i>	Unknown	D	0-5	1.60	6-18	16.25	0-2	0.30	0-6	1.25	38.00
		M	0-6	2.00	6-18	16.75	0-1	0.10	0-6	1.05	36.30
<i>Paspalum simplex</i>	Australia	M	0-2	0.25	6-19	16.47	0-2	0.07	0-7	1.65	36.55
<i>Pennisetum pedicellatum</i>	Poona India	D	0-2	0.20	9-18	15.10	—	—	0-3	1.40	34.10
		M	0-2	0.20	9-16	16.50	—	—	0-2	0.70	32.50
<i>Urochloa mo- sambicensis</i>	Australia	D	—	4.60	—	10.00	—	0.75	—	0.30	21.20
		M	—	5.50	—	9.40	—	0.70	—	0.40	16.37
<i>Urochloa pullulans</i>	Africa	D	—	3.30	—	8.1	—	1.10	—	1.30	21.50
		M	—	6.70	—	6.8	—	1.50	—	0.80	16.37

Digitaria Heist ex Fabricius

This genus composed of 100 species is distributed in the warmer parts of the world. Some species are very good for forage. Cytologically, they form an interesting group and several species have been studied in detail.

D. adscendens (H. B. K.) Henr.

An Australian entry of this species showed 36 somatic chromosomes. Counts of $2n=36$ (Nath and Swaminathan 1957), 54 (Tateoka 1953, Chen and Hsu 1961, Gould 1963) and 60 (Mulay and Leelamma 1956) have been

recorded. This suggests intraspecific polyploidy in the species.

At diakinesis and metaphase I, 18 bivalents were generally observed. Most bivalents were of ring type. Occasional cells showed one or two rod bivalents. Meiosis was regular. Pollen fertility and seed set were 98 and 96 per cent, respectively.

Digitaria sanguinalis is very closely related to *D. adscendens* (H. B. K.) Henr. and *D. chinensis* Horn. Bor (1960) has regarded *D. chinensis* as a synonym of *D. adscendens*; *D. sanguinalis* and *D. adscendens* have been treated as synonymous by some American botanists (c.f. Ebinger 1962). Taxonomic interpretation of species named has caused some confusion in cytological records. Numbers $2n=36$ and 54 were reported for *D. sanguinalis* s. str. and *D. adscendens* (Tateoka 1965 b). This species complex is worthy of detailed biosystematic study.

D. eriantha Steud.

An entry from S. Africa possessed 36 somatic chromosomes. Previous reports of $2n=18$ (Moffett and Hurcombe 1949), 36 (Nath and Swaminathan 1957) and 40 (de Wet 1954) for this species indicate the presence of intra-specific polyploidy.

At diakinesis and metaphase I, 18 bivalents were counted in several cells, (Fig. 11). Meiosis was slightly irregular. Mean chiasma frequencies per bivalent at diakinesis and metaphase I were 2.0 and 1.91, respectively. At anaphase I, 17 per cent of the cells showed 1-4 lagging chromosomes (average of 0.3 per cell). The lagging chromosomes occasionally divided at anaphase I. Lagging chromosomes (1-2) were also observed at anaphase II. Pollen fertility was 84 per cent. Regular occurrence of 18 bivalents in this tetraploid race ($x=9$, c.f. Moffett and Hurcombe 1949) suggests its allopolyploid origin unless the formation of bivalents is genotypically controlled.

Of special interest was a plant of *D. eriantha*, which exhibited the phenomenon of breakdown of meiosis (Figs. 12-18). This plant was morphologically indistinguishable from the rest.

The pollen mother cells at early prophase were without well differentiated cell walls. Thus several nuclei were included in a common mass of cytoplasm. These cytoplasmic masses were of varying sizes and shapes, some were irregular in their outline, others were quite regular. The number of nuclei in these cenocytes varied from 2-17. Similar cenocytes have been reported in *Phleum pratense* by Nath and Nielsen (1961). The appearance of premeiotic errors in inbred rye lines resulted in atypical chromosome behaviour (Rees 1957). Other nuclear behaviours that could be similarly interpreted have been suggested to be associated with inbreeding in brome grass (Nielsen 1960). Coenocytes may originate as a result of pre-meiotic errors (Rees 1957). The coenocyte formation in rye lines and timothy appeared to be controlled recessively (Rees 1957, Nielsen 1960).

The nuclei in the cytoplasmic masses were characterized by a different

Figs. 11-18. Meiosis in *Digitaria eriantha* (Magnification 1065 $\times$). 11, metaphase I with 18 bivalents. 12, coenocyte with numerous nuclei (note the prominent nucleoli). 13, 18 bivalents. 16, coenocyte with numerous nuclei (note the prominent nucleoli).

degree of carmine stainability. In some cells, they hardly stained at all and appeared very faint. It is tempting to suppose that these are interphase nuclei, but comparisons with the normal nuclei suggests that these may be degenerated nuclei.

In the second type of nuclei, the chromosomes at this stage, though not distinguishable as separate entities, were better stained. Chromosomes in some nuclei appeared fragmented. Chromosome fragments could be clearly seen at later stages. In one such cell, 81 fragments surrounding a mass of chromosomes could be clearly counted. No chromosome pairing was, however, observed and it seems that metaphase stage was never reached. The chromosome fragments were often crowded together and appeared to form a restitution nucleus.

The third type of nuclei, which were more or less regular in their appearance at early prophase, showed normal development of chromosomes so that a metaphase plate was often formed. In some cenocytes, however, a failure of pairing was observed and in such cases the spindle was never organized. However, in those cytoplasmic masses in which the nuclei reached metaphase I, each of these nuclei formed a spindle of its own. In some cases, the chromosomes from different nuclei came together to be oriented on a single spindle and a metaphase plate with a large number of chromosomes was formed. In still other cases, some chromosomes from different nuclei came together on a common spindle, while others remained scattered, failing to be arranged on the spindle. Subsequent stages were not noticed.

Eriochloa Kunth

This genus is widespread in the warmer parts of both hemispheres. Its spikelets have distinct callus to which the lower glume is adnate. Its inflorescences are composed of racemes along a common axis.

E. nubica (Steud.) Hack. et Stapf ex Thell

An East African entry had 36 somatic chromosomes. Earlier reports are in agreement with this count (Nath and Swaminathan 1957, de Wet 1960, Tateoka 1965 a, b). Singh and Godward (1960) reported $2n=18$ for a collection of this species from Kenya, thus suggesting intraspecific polyploidy.

At diakinesis and metaphase I, 18 bivalents were regularly formed (Fig. 19). Chiasma frequencies per bivalent at diakinesis and metaphase I were 1.98 and 1.82, respectively. One or two lagging chromosomes were observed in 10 per cent of the cells. Pollen fertility and seed set were almost 100 per cent.

coenocyte with three nuclei at diakinesis (note the fragmented nature of chromosomes). 14, metaphase I with a mass of chromatic material in the center and fragmented chromosomes scattered around it. 15, coenocyte with several metaphase I plates. 16, coenocyte with a single metaphase I plate (note fragmented chromosomes). 17, coenocyte with unoriented metaphase I plate (note extreme fragmentation of chromosomes). 18, coenocyte with four metaphase I plates apparently on separate spindles.

Figs. 19-27. Meiosis in Paniceae (Magnification 1065 $\times$). 19, diakinesis in *Eriochloa nubica* showing 18 bivalents. 20, diakinesis in *Paspalum simplex* showing 4 quadrivalents and 12 bivalents. 21, diakinesis in *Paspalum vaginatum* showing 10 bivalents. 22, diakinesis in *Pennisetum pedicellatum* showing 2 quadrivalents and 14 bivalents. 23, late

E. pseudoacrotricha (Staph ex Thell.) Hubb. ex Blake

This species is not so leafy and hence not good for forage. At diakinesis and metaphase I, 18 bivalents were noticed. Chiasma frequencies per bivalent at these two stages were 2.0 and 1.9, respectively. Pollen fertility and seed set were almost 100 per cent.

Panicum Linn.

The genus composed of more than 500 species is distributed in tropics and subtropics of both hemispheres. Some species also grow in warm, temperate regions. Hartley (1958) concluded that the distribution of the tribe Paniceae shows a close relationship to higher winter temperature and, especially to fairly well distributed rainfall. Stapf (1920) studied more than 100 species of *Panicum* in tropical Africa. The members of the specialized group *Dichantherium*, containing about 120 species, are confined to the Atlantic coast of North America and form another center of origin of *Panicum*. The third center represented only by a few species occurs both in tropical America and Asia. It seems that no endemic section occurs in Australia.

P. cymbiforme Hughes

The species showed $2n=18$ chromosomes at meiosis, as reported by Nath and Swaminathan (1957) and Jauhar Joshi (1966a). At diakinesis and metaphase I, a regular formation of 9 bivalents was observed. The mean chiasma frequency per cell at metaphase I was 16.4. The remaining stages of meiosis were regular. Pollen fertility was 100 per cent. Seed set was 98 per cent.

P. laevifolium Hack.

An entry from S. Africa had 18 somatic chromosomes. Nine bivalents were regularly formed at diakinesis and metaphase I. At prophase, two bivalents were attached to a large, densely staining nucleolus in most cells. Chiasma frequencies per bivalent at diakinesis and metaphase I were 2.0 and 1.92, respectively. The pollen fertility and seed set were 96 and 98 per cent, respectively.

P. maximum Jacq.

This polymorphic species widely distributed in the tropics has been studied in detail. Its reported somatic chromosome numbers are 18 (de Wet 1954, Raman *et al.* 1959), 32 (Moffett and Hurcomb 1949, Warmke 1951, Chandola 1959, Chen and Hsu 1961, Tateoka 1965a, Jauhar 1967), 36 (Pienaar 1955, Raman *et al.* 1959), 44 (Moffett and Hurcombe 1949) and 48 (Warmke 1951).

Six entries, viz., one from Australia, two from Brazil and three from

anaphase I in *Pennisetum pedicellatum* showing 54 chromosomes. 24, telophase I showing several lagging chromosomes in an entry from Australia of *Pennisetum pedicellatum*. 25, late anaphase I showing 13-15 distribution of chromosomes to the two poles in *Urochloa mosambicensis*. 26, anaphase I showing 5 lagging chromosomes in *Urochloa mosambicensis*. 27, metaphase I in *Urochloa pullulans* showing 2 quadrivalents, 7 bivalents and 6 univalents.

India were studied. One entry from Brazil had 18 somatic chromosomes and the rest had $2n=32$.

In the diploid entry from Brazil, a regular formation of nine bivalents was observed. Meiosis was regular. Pollen fertility and seed set were 97 and 92 per cent, respectively.

Chromosome associations and chiasma frequencies during diakinesis and metaphase I were studied in detail in five entries (Table 1). Multivalents were observed besides bivalents and univalents. The entries differed in the number of mean chromosome associations and the chiasma frequencies during these stages. At anaphase and telophase I, irregular distribution of chromosomes to the two poles, dividing and non-dividing lagging chromosomes (1-7) and chromosome bridges and fragments were observed. The frequencies of these irregularities varied in different entries. Lagging chromosomes were also observed during anaphase and telophase II. Persistent nucleoli were noticed in the Australian strain even at anaphase and telophase II. Pollen fertility and seed set varied from 46-85 per cent.

Somatic chromosome numbers 18, 32, 36, 44 and 48 reported in different collection of *P. maximum* suggest the presence of intraspecific polyploidy. Raman *et al.* (1959), who reported $2n=18$ for this species noted that the meiotic division was regular, as also observed in this study on a Brazilian entry. Warmke (1951), Chandola (1959) and Chen and Hsu (1961) found various combinations of quadrivalents, trivalents, bivalent and univalents at meiosis in plants with $2n=32$ chromosomes.

Predominance of $x=9$ for the entire genus *Panicum* suggests that in *P. maximum*, $x=8$ was derived from a higher number and possibly from forms with $x=9$ (Jauhar and Joshi 1966 c). This interpretation appears varied because the diploid form is reported to possess $2n=18$ and the tetraploid $2n=36$. Entries with $2n=32$ chromosomes seem to have arisen due to autopolyploidy followed by chromosome elimination and structural changes in the basic genomes. Plants with 32 somatic chromosomes could also originate by the fusion of gametes carrying 18 and 14 chromosomes (Jauhar and Joshi 1966 c). Plants with $2n=32$ chromosomes have been maintained in the population through apomixis. High degree of seed set in several entries suggests the presence of apomixis. In fact, Warmke (1951) first indicated the presence of apomixis and later showed that both apospory and pseudogamy exist in this species. Warmke (1954), Brown and Emery (1958) also found this species highly apomictic. Jauhar and Joshi (1966 b) recognized 5 distinct morphological types among 20 collections of this species. This enormous variability seems to have been maintained in nature due to apomixis.

Paspalum Linn

The genus composed of about 200 species is distributed mostly in the Americas especially Brazil. The racemose inflorescence and the absence of lower glume serve as diagnostic generic characters. In this genus, the upper

florets have well developed transverse and longitudinal ridges and, the papillae on the depressions are longitudinally arranged in regular rows.

P. orbiculare Forst

The species is distributed in Southeast Asia. One entry from Palampur, India had 54 somatic chromosomes. Tateoka (1956) and Hsu (1965) reported $2n=60$ chromosomes in the material studied by them. At diakinesis and metaphase I, and univalents (2-12) and bivalents (21-26) were observed (Table 1). The chiasma frequencies (per cell) at these two stages were 45.9 and 43.5, respectively. Successive stages were not analyzed. Pollen fertility and seed set were 35 and 10 per cent, respectively.

The high number of univalents may be due to desynapsis. Since in several cells some chromosomes are paired, desynapsis may be placed in the "medium-strong" class of Prakken (1943). Similar desynaptic behavior has been reported in several other grasses (Li *et al.* 1955, Krishnaswamy and Meenakshi 1957, Celarier and Mehra 1959). The genetics of desynapsis seems surprisingly simple and in all cases studied it appears to result from the recessive condition of one or a few genes (Beadle 1930, Clausen 1931, Bergner *et al.* 1934, Richardson 1935, Beasley and Brown 1942, Prakken 1943, Johnson 1944, Li *et al.* 1945, Celarier 1955, Krishnaswamy and Meenakshi 1957).

P. plicatum Michx.

The species is distributed in U.S.A., southwards through Brazil to Argentina and throughout the West Indies. One entry from an unknown source had $2n=40$ chromosomes. Earlier chromosome counts for this species are $2n=40$ (Brown 1950), 40 (Saura 1948, Pritchard and Gould 1964) and 60 (Pritchard and Gould 1964). Thus intraspecific chromosome races exist in this species.

At diakinesis and metaphase I, multivalents and univalents were noticed besides bivalents (Table 1). At diakinesis, most cells had only one nucleolus but a few had two. The mean chiasma frequencies per cell were 38.0 and 36.3 at diakinesis and metaphase I, respectively (Table 1). A maximum of six quadrivalents were observed in a few cells at these stages. Large numbers of pycnotic droplets were observed in a few cells at anaphase and telophase I. The size and number of such droplets varied in different cells. The origin and function of such bodies is not yet clear. Similar droplets have been reported in *Phleum pratense* (Nath and Nielsen 1961). Pollen fertility was 87 per cent. The presence of 6 quadrivalents would suggest its autotetraploid origin with $x=10$ chromosomes.

P. simplex Morang

One entry from Australia had 40 somatic chromosomes. At diakinesis and metaphase I, quadrivalents, bivalents and univalents were seen (Fig. 20, Table 1). A maximum of 7 quadrivalents were observed in one cell. Mean chiasma frequency per cell at diakinesis was 36.55. Meiosis was slightly irregular. Pollen fertility was only 60 per cent. The presence of 7 quadri-

valents points to its autotetraploid origin with $x=10$ chromosomes.

P. vaginatum Swartz.

The species is distributed in the tropics and subtropics of the whole world. An entry from Australia showed 20 somatic chromosomes. This count agrees with other reports (Avdulov 1931, Brown 1948, Tateoka 1962, 1965 a). The bivalents were observed at diakinesis and metaphase I (Fig. 21). Mean chiasma frequencies per bivalent at these stages were 1.98 and 1.96, respectively. Meiosis was normal. The pollen fertility was 80 per cent. Seed set was over 90 per cent.

Pennisetum Rich.

This genus composed of 50 species is distributed in the tropical regions of both hemispheres. Most of the species are African. The genus possesses a cylindrical spike-like panicle. The spikelets are solitary or in 2-3 fascicles, subtended by an involucre composed of bristles. The involucres fall off entirely together with the spikelets and the scars remain on the main axis of the inflorescence. The upper floret is more or less spinose espically towards the apex.

P. pedicellatum Trin.

This species is distributed in tropical Africa and India. Two entries, one from Poona, India and the other from Australia were studied.

a) Poona entry

This entry had $2n=36$ chromosomes. Quadrivalents and univalents were observed besides bivalents at diakinesis and metaphase I (Fig. 22, Table 1). Chiasma frequencies per cell during these stages were 30.83 and 28.60, respectively. Micronuclei were observed in one-third of the cells examined at dyad stage. The average number of micronuclei per dyad was 0.48. Pollen fertility was 78.7 per cent. Seed set was very poor.

b) Australian entry

This entry had $2n=54$ chromosomes (Fig. 23). Diakinesis and metaphase I could not be studied in detail. However, the cells, that could be analyzed, showed 0-3 quadrivalents. At anaphase and telophase I, 80 per cent of the cells had 1 to 12 lagging chromosomes (Fig. 24). Micronuclei (1-6) were observed in 60 per cent of the cells. Pollen fertility and seed set were 40 and 60 per cent, respectively.

Nath and Swaminathan (1957) reported $2n=36$ and 54 chromosomes in this species, while Joshi *et al.* (1959) reported $2n=48$ chromosomes. This suggests intraspecific polyploidy in the species. Little is known about the taxonomic status of these taxa. Detailed cytotaxonomical studies are needed to establish the basic chromosome number of this species-complex.

Urochloa P. Beauv.

This genus, composed of annual and perennial species, is distributed in the warmer parts of the old world. A few species, i.e., *U. mosambicensis*

(Hack.) Dandy and *U. pullulans* Stapf are very much valued as forage grasses. The genus is distinguished from *Brachiaria* by abaxial spikelets.

U. mosambicensis (Hack.) Dandy

It is a perennial grass widely distributed in Africa. An entry from Australia showed $2n=28$ chromosomes (Fig. 25). This count confirms the reports of Raman *et al.* 1959. However, de Wet and Anderson (1959) reported $2n=30$ chromosomes and Moeffett and Hurcombe (1949) observed $2n=42$ chromosomes in the materials studied by them.

At diakinesis and metaphase I, multivalents bivalents and univalents were observed (Table 1). Almost all cells had multivalents. Mean chiasma frequencies per cell at diakinesis and metaphase I were 26.2 and 22.87 respectively. At anaphase I, 67 per cent of the cells showed irregular distribution of chromosomes to the two poles. Lagging chromosomes (Fig. 26), chromosome bridges and fragments were observed, though their frequencies were low. Lagging chromosomes were seen at anaphase and telophase II. Pollen fertility was 60 per cent but seed set was very low. Detailed cytotaxonomic studies would clarify the basic chromosome number of the species since plants with $2n=28$, 30 and 42 chromosomes have been reported.

U. panicoides P. Beauv. var. *pubescens* (Kunth.) Bor.

An entry from West Bengal, India had $2n=36$ chromosomes. Other counts reported for this species are $2n=24$ (Raman *et al.* 1959), 30 (de Wet 1954) and 36 (Moffett and Hurcombe 1949).

Almost all cells at diakinesis and metaphase I, had some univalents. Chiasma frequencies per bivalent during these stages were 1.71 and 1.49, respectively. At anaphase and telophase I, several irregularities, i.e., unequal distribution of chromosomes to the poles, lagging chromosomes (1-7) and dividing univalents were encountered in 30 per cent of the cells studied. The average number of lagging chromosome per cell was 1.17. Pollen fertility and seed set were 86 and 74 per cent, respectively.

Somatic chromosome numbers 24, 30 and 36 reported in different collections of this species suggest the presence of intraspecific polyploidy. Little is known about the taxonomic status of these taxa. Detailed cytotaxonomical studies will throw light on the basic chromosome number ($x=8$, 9, or 10) of this species.

U. pullulans Stapf

This species is distributed in tropical Africa, and has 28 chromosomes (Moffett and Hurcombe 1949, Tateoka 1965 a, b). Two entries, one each from Australia and Africa had 28 somatic chromosomes. Meiosis in both entries was essentially regular. At diakinesis and metaphase I, quadrivalents, bivalents and univalents were observed (Table 1, Fig. 27). One cell at metaphase I in the African entry contained one pentavalent, one trivalent, five bivalents and ten univalents. Quadrivalents and trivalents were either open or ring type. At anaphase and telophase I, 1-9 lagging chromosomes

(dividing and non-dividing) were observed. Pollen stainability was 59 and 51 per cent in the African and Australian materials, respectively. The seed set was practically nil in both of them.

Review of literature (Carnahan and Hill 1961) on the chromosome numbers of grasses revealed that out of 2300 species of grasses for which the chromosome numbers are known, about 80% are probably polyploid, with 7% of these aneuploid, the other 20% are diploid. This study indicates the presence of aneuploidy and intraspecific polyploidy in *Brachiaria brizantha* ($2n=18, 36, 54$), *Cenchrus ciliaris* ($2n=32, 34, 35, 36, 40, 43, 44, 48, 52, 54, 56, 78$), *Digitaria adscendens* ($2n=36, 54, 60, 72$), *D. eriantha* ($2n=18, 36, 40$), *Eriochloa nubica* ($2n=18, 36$), *Panicum maximum* ($2n=18, 32, 36, 44, 48$), *Paspalum orbiculare* ($2n=54, 60$), *P. plicatulum* ($2n=20, 40, 60$), *Pennisetum pedicellatum* ($2n=36, 48, 54$), *Urcuhloa mosambicensis* ($2n=28, 30, 42$) and *U. panicoides* ($2n=30, 36, 48$).

Cytological findings reported herein are similar to those observed by other workers in members of Paniceae (Carnahan and Hill 1961). The interesting features are the presence of intraspecific polyploidy, variation in chromosome numbers and apomixis. In polyploid taxa, multivalents and univalents were observed besides bivalents at metaphase I of meiosis. Also, irregular distribution of chromosomes, dividing univalents, chromosome bridges and fragments were observed at anaphase I. Meiotic irregularities were rare in the diploids but common in polyploids. Apomictic mode of reproduction has been reported in several genera of Paniceae (see review of Carnahan and Hill 1961). Also, the majority of these grasses are multiplied by vegetative means. Polyploidy and chromosomal irregularities render apomixis both possible and predominant in many genera (Gustafsson 1947). Thus, it appears that the various abnormalities observed in the material studied are associated with polyploidy, hybridization and apomixis.

Meiotic studies in several species showed that the chromosomes in them can associate to form multivalents at metaphase I. This indicates that some of the chromosomes (or chromosome segments) are homologous. The question arises whether such polyploid types arose by segmental allopolyploidy, by auto-allopolyploidy or be autopolyploidy followed by long periods of chromosome and genetic differentiation. Stebbins (1947, 1950) has described in great detail the occurrence and characteristics of polyploids, and has also pointed out the difficulties in classifying them. Chromosome associations at the first division of meiosis are the usual source of information concerning the type of polyploidy in a given plant. The presence of multivalents is considered as an indication of autopolyploidy and its absence of allopolyploidy. (Stebbins 1950). However, absence of multivalents in a species may be due to a special genotypically controlled tendency to form only bivalents (Müntzing and Prakken 1940, Nordenskiöld 1940). Recently, experimental support for such a theoretical suggestion has been presented in wheat (Riley and Chapman

1958, Sears and Okamoto 1958) and *Bothriochloa-Dichanthium* complex (Chheda and Harlan 1962, Mehra and Singh 1968). The frequencies of quadrivalents in *Cenchrus ciliaris*, *Paspalum plicatulum* and *Paspalum simplex* seem to be high enough to suggest their autopolyploid origin. In the rest of the material studied, the quadrivalent frequency was low. In such cases, the factors favoring the accumulation of chromosome structural changes seem to be in operation.

Though polyploidy has been recognized in nearly half of the members of plant kingdom, intraspecific polyploidy has been reported for less than 7% of the species of Angiosperms, and more than 90% of these polyploid types or chromosome races have been described as distinct species. Löve (1951) examined thirty reported examples of intraspecific polyploidy among Northern European plants and concluded that all chromosome races, except those which are asexually propagated, should be recognized as distinct species even if morphological differences among such races are slight. It is mostly due to the fact that on detailed examination several chromosome races have been found to be distinct morphologically and genetically. Stebbins (1950) has cited several instances to show that even allopolyploids derived from hybridization between species having widely different chromosome homologies, may resemble one or the other parental species so closely that they could not be recognized as distinct taxa by taxonomists. Typical allopolyploids appear to be rare in nature and consequently real intraspecific chromosome races may not occur except in apomicts. No morphological data were recorded on the different chromosome races of the material studied. The problem of evaluating the precise taxonomic status of the chromosome races reported herein needs careful consideration. Also, detailed study of the ecological adaptability of the chromosome races would be essential in making proper recommendations on the suitability of a specific chromosome race of a species for a specific agro-climatic tract.

Summary

Chromosome numbers were determined during microsporogenesis in strains belonging to 21 species and 8 genera of Paniceae. These include 4 new reports. Intraspecific chromosome races were found in *Brachiaria brizantha*, *Cenchrus ciliaris*, *Digitaria adscendens*, *D. eriantha*, *Eriocloa nubica*, *Panicum maximum*, *Paspalum orbiculare*, *P. plicatulum*, *Pennisetum pedicellatum*, *Urochloa mosambicensis* and *U. panicoides*.

Meiosis was studied in all species. Chromosome pairing was regular in diploids but irregular in polyploids and aneuploids. It is suggested that polyploidy and meiotic irregularities are mechanisms which favor apomictic mode of reproduction in the members of Paniceae studied herein. The frequencies of quadrivalents observed in strains of *Cenchrus ciliaris*, *Paspalum plicatulum* and *Paspalum simplex* seem to be high enough to suggest their

autopoloid origin. In the rest of the species with low quadrivalent frequency, the factors favoring the accumulation of chromosome structural changes seem to be in operation.

Of special interest was a plant of *Digitaria eriantha*, which exhibited the phenomenon of breakdown of meiosis. The pollen mother cells at early prophase were without well differentiated cell walls, due to which several nuclei formed cenocytes. A few cells showed fragmentation of chromosomes. The metaphase stage was never reached. The fragmented chromosomes formed restitution nuclei. A few cells formed multiple spindles. The pollen fertility was very low.

The significance of the cytological findings was discussed.

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