

The presence of synaptic and chromosome disjunction mutants in *Cenchrus ciliaris* (Poaceae: Paniceae)

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ABSTRACT

Synaptic mutants are present in *Cenchrus ciliaris* L. This species, due to the presence of linear bivalents and occasional trivalents and quadrivalents, is an intermediate desynaptic species. In addition, geographical distribution and environmental factors, such as high temperatures and low humidity, could also have had an influence on the desynapsis observed. The disjunction of chromosomes during anaphase I was mostly abnormal in this desynaptic species. Precocious disjunction of chromosomes into chromatids occurred during anaphase I. Due to the high incidence of this chromosome abnormality, a mutant gene, 'pc', responsible for the disjunction of chromosomes, must be present. The absence of cytokinesis in one specimen indicates a recessive mutant gene, 'va', to be active in this species.

INTRODUCTION

Meiosis is a complex process and includes cytogenetic features such as chromosome pairing, synaptonemal complex formation, recombination, chromosome segregation and the creation of gametic meiotic products. The precise sequence of meiosis is under the control of various genes (Golubovskaya 1979). These include premeiotic genes, 'as' genes (controlling leptotene and zygotene), 'des' genes (controlling the various stages from pachytene to metaphase I) and chromosomal disjunction or spindle genes (controlling meiotic stages from anaphase I through to the formation of tetrads) (Golubovskaya 1979). Mutations present in these genes drastically change the normal behaviour of chromosomes within a specimen or species. Reports of synaptic and male-sterility mutants predominate, whereas premeiotic and disjunction mutants are relatively rare (Singh 1993).

Synaptic mutants are common in the plant kingdom and were originally discovered in maize ($2n = 20$) (Beadle & McClintock 1928) and were observed in about 20 higher plant families, consisting of 50 genera and approximately 70 species (Koduru & Rao 1981). The majority of these taxa belong to the family Poaceae (Singh 1993).

Meiotic mutants have been mainly identified with the aid of cytogenetic studies, genetic evidence and pollen or ovule abortion. These mutants, which arise mostly spontaneously, may result from interspecific hybridisation or may be induced by mutagenesis (Singh 1993). The aim of this study was to determine whether meiotic mutants are present in *Cenchrus ciliaris* L.

MATERIALS AND METHODS

The specimens used are listed in Table 1. Voucher herbarium specimens are housed in the George Potts

Herbarium, Department of Botany and Genetics, University of the Orange Free State, Bloemfontein (BLFU). Slides, suitable for meiotic studies, were prepared according to the methods described by Visser & Spies (1994). A minimum of 20 cells of each of the following stages were studied: metaphase I, anaphase I, and telophases I and II. The following were recorded when observed: chromosome configurations and the number of univalents (MI), laggards (AI) and micronuclei (TI and TII).

RESULTS AND DISCUSSION

Cytogenetic results were recorded for 76 specimens (Table 1). Polyploidy is common and includes three levels, namely tetraploid ($n = 2x = 18$; 82.9%), pentaploid ($n = 5/2x = 45/2$; 9.2%) and hexaploid ($n = 3x = 27$; 6.6%).

Cells in the diakinesis stage were seldom observed. Well-defined meiotic configurations during diakinesis were observed in one specimen only, *Spies 5655* (Figure 1A). The chromosomes were small and configurations consisting of more than one chromosome, were identified based on relative size (Figure 1A–D). The chromosomes were often not paired and were distributed as univalents in the cell (Figure 1A–D).

Meiotic behaviour of the various chromosome configurations observed, varied during metaphase I (Figure 2A–E). Bivalents and occasional trivalents or quadrivalents moved to the equatorial plate, whereas the univalents were mostly distributed in the cytoplasm (Figure 2A–E). The number of univalents observed during metaphase I, varied within the different microsporocytes in the same specimen. In *Spies 5230*, zero to 18 univalents were observed during metaphase I (Table 1). This was the highest number of univalents observed within a single cell of this species (Table 1). More than 95% of the univalents observed were two or multiples of two per cell (Visser *et al.* 1998a), indicating that they originate from incomplete pairing of a chromosome pair, rather than representing the odd non-pairing chromosome in multivalent formation.

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TABLE 1.—Meiotic chromosome behaviour of *Cenchrus ciliaris* specimens. The voucher numbers, their quarter degree grid references, gametic chromosome numbers and meiotic chromosome behaviour are indicated

Voucher number	Grid	Gametic chromosome number	% Metaphase I cells containing univalents	% Anaphase I cells with precocious chromatid segregation	1	2	3	4	5	6	7	8	9	10	11	12	13	15
<i>Spies 5883</i>	2627CA	17	62 (0-4)	50	10	10	20	10	-	-	-	-	-	-	-	-	-	-
<i>Spies 5215</i>	3224DD	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5226</i>	3320DC	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5229</i>	3325CD	18	100 (1-3)	75	17	-	33	8	-	8	8	-	-	-	-	-	-	-
<i>Spies 5230</i>	3325CD	18	88.9 (0-18)	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5231</i>	3324DA	18	16.7 (0-2)	62.4	19	13	6	11	6	6	6	-	-	-	-	-	-	-
<i>Spies 5232</i>	3324BD	18	40 (0-10)	50	20	10	20	6	19	-	-	-	-	-	-	-	-	-
<i>Spies 5236</i>	3224DC	18	14.3 (0-4)	82	27	46	9	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5237</i>	3224DC	18	20 (0-2)	56	13	6	25	6	-	-	6	-	-	-	-	-	-	-
<i>Spies 5240</i>	3224BC	18	90 (0-8)	63.5	-	9	18	9	9	9	-	9	-	-	-	-	-	-
<i>Spies 5487</i>	3222BC	18	40 (0-2)	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5488</i>	3222BC	18	44.4 (0-2)	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5489</i>	3222BC	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5508</i>	2925AB	18	23 (0-4)	66	22	22	22	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5509</i>	2925AA	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5512</i>	2925AA	18	25 (0-6)	36.4	-	-	-	-	9	18	9	-	-	-	-	-	-	-
<i>Spies 5521</i>	2822DA	18	30 (0-6)	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5522</i>	2724AB	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5525</i>	2723BC	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5527</i>	2724AB	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5529</i>	2624DC	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5531</i>	2624DC	18	83.3 (0-6)	18	-	9	-	-	9	-	-	-	-	-	-	-	-	-
<i>Spies 5538</i>	2725AA	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5539</i>	2725AA	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5542</i>	2725AA	18	37.5 (0-5)	44	-	-	44	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5543</i>	2725CB	18	100 (1-4)	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5553</i>	2825BB	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5574</i>	2826CD	18	20 (0-1)	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5575</i>	2826CD	18	77.8 (0-4)	21.3	-	7	7	-	7	-	-	-	-	-	-	-	-	-
<i>Spies 5576</i>	2826CD	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5577</i>	2826CD	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5584</i>	3125BC	18	50 (0-8)	61	8	16	8	14	8	7	-	-	-	-	-	-	-	-
<i>Spies 5585</i>	3125BC	18	40 (0-2)	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5586</i>	3125BC	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5587</i>	3125DC	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5591</i>	3225DB	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5594</i>	3225DB	18	*	56	14	14	-	14	14	-	-	-	-	-	-	-	-	-
<i>Spies 5638</i>	2826CD	18	57 (0-4)	75	-	25	25	-	25	-	-	-	-	-	-	-	-	-
<i>Spies 5642</i>	2926AA	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5643</i>	2926AA	18	0	10	-	-	-	10	-	-	-	-	-	-	-	-	-	-
<i>Spies 5645</i>	2528CC	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5646</i>	2628AB	18	57.1 (0-8)	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5649</i>	2727AC	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5650</i>	2727AC	18	64 (0-8)	20	-	-	-	10	10	-	-	-	-	-	-	-	-	-

* Insufficient number of metocytes of the particular meiotic stage studied.

TABLE 1.—Meiotic chromosome behaviour of *Cenchrus ciliaris* specimens. The voucher numbers, their quarter degree grid references, gametic chromosome numbers and meiotic chromosome behaviour are indicated (cont.)

Voucher number	Grid	Gametic chromosome number	% Metaphase I cells containing univalents	% Anaphase I cells with precocious chromatid segregation	1	2	3	4	5	6	7	8	9	10	11	12	13	15
<i>Spies 5652</i>	2627CD	18	100 (1-4)	36	-	18	-	9	9	-	-	-	-	-	-	-	-	-
<i>Spies 5653</i>	2627CA	18	75 (0-4)	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5654</i>	2627CA	18	66.6 (0-5)	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5655</i>	2626DD	18	33.3 (0-3)	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5657</i>	2726DA	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5659</i>	2726CD	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5660</i>	2826BB	18	62.5 (0-4)	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5662</i>	2826AA	18	60 (0-4)	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5664</i>	2926AA	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5668</i>	3125BC	18	62.5 (0-4)	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5669</i>	3125BC	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5670</i>	3125BC	18	100 (2-4)	10	-	-	-	10	-	-	-	-	-	-	-	-	-	-
<i>Spies 5671</i>	3125DC	18	20 (0-2)	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5675</i>	3225DB	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5676</i>	3225DB	18	0	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5847</i>	2926AA	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5848</i>	2926AA	18	87.5 (0-4)	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5849</i>	2826CD	18	50 (0-4)	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5850</i>	2826CD	18	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ventier 9286</i>	2732CC	18	85.7 (0-4)	40	10	10	-	20	-	-	-	-	-	-	-	-	-	-
<i>Du Prez 2758</i>	2925AD	45/2	•	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5210</i>	3224DD	45/2	100 (3-8)	100	-	-	-	-	-	-	83	-	17	-	-	-	-	-
<i>Spies 5238</i>	3224DC	45/2	100 (1-10)	100	-	-	-	-	-	-	-	9	36	-	9	9	18	18
<i>Spies 5239</i>	3224DA	45/2	•	100	-	-	-	-	-	25	-	25	-	25	-	25	-	-
<i>Spies 5497</i>	2522DB	45/2	100 (2-8)	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5581</i>	3024DA	45/2	•	100	-	-	-	-	-	-	17	8	-	8	8	8	25	25
<i>Spies 5583</i>	3024DA	45/2	•	100	-	-	-	-	9	-	-	18	18	-	27	27	-	-
<i>Spies 5510</i>	2824DA	27	100 (2-7)	66	11	22	11	-	-	11	-	11	-	-	-	-	-	-
<i>Spies 5513</i>	2824DA	27	•	39	13	-	13	13	-	-	-	-	-	-	-	-	-	-
<i>Spies 5514</i>	2824DA	27	67 (0-8)	73	-	9	-	9	9	18	9	9	9	-	-	-	-	-
<i>Spies 5515</i>	2824DA	27	63 (0-5)	30	-	-	30	-	-	-	-	-	-	-	-	-	-	-
<i>Spies 5517</i>	2824DA	27	67 (0-3)	66	11	-	11	22	-	-	11	-	-	11	-	-	-	-

• Insufficient number of meiocytes of the particular meiotic stage studied.

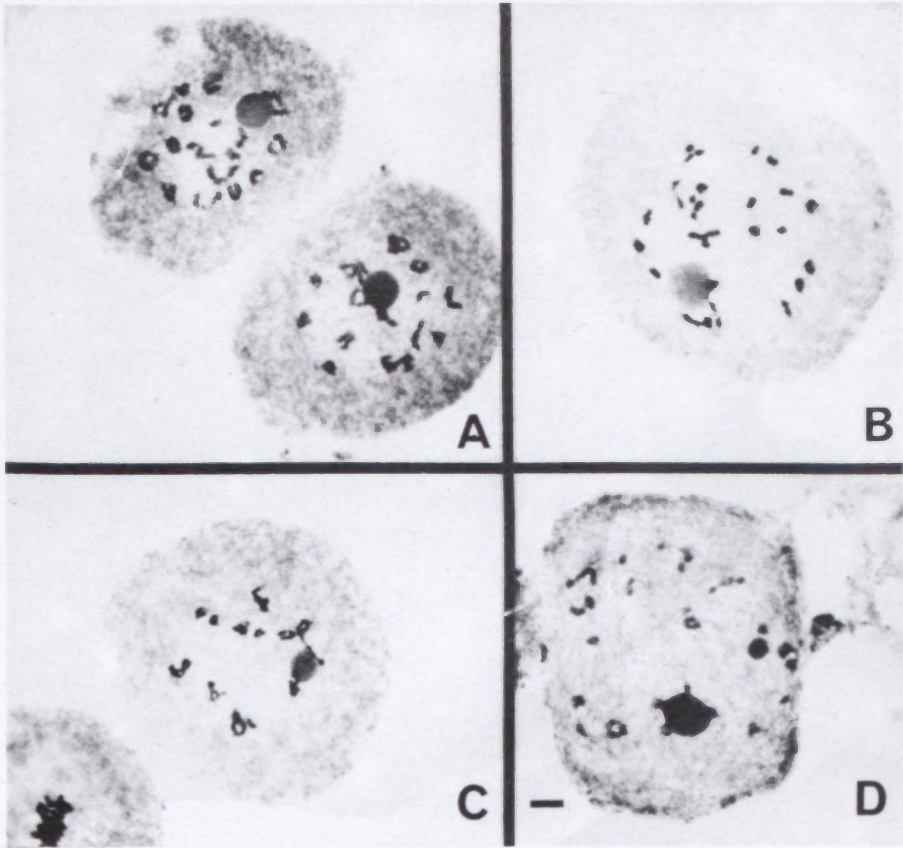


FIGURE 1.—Photomicrographs of *Cenchrus ciliaris* meiocytes during diakinesis, indicating the lack of well-defined meiotic configurations and the presence of univalents. A, *Spies* 5655, $n = 18$; B, *Spies* 5574, $n = 18$; C, *Spies* 5583, $n = 45/2$; D, *Spies* 5517, $n = 27$. Scale bar: 10 μm .

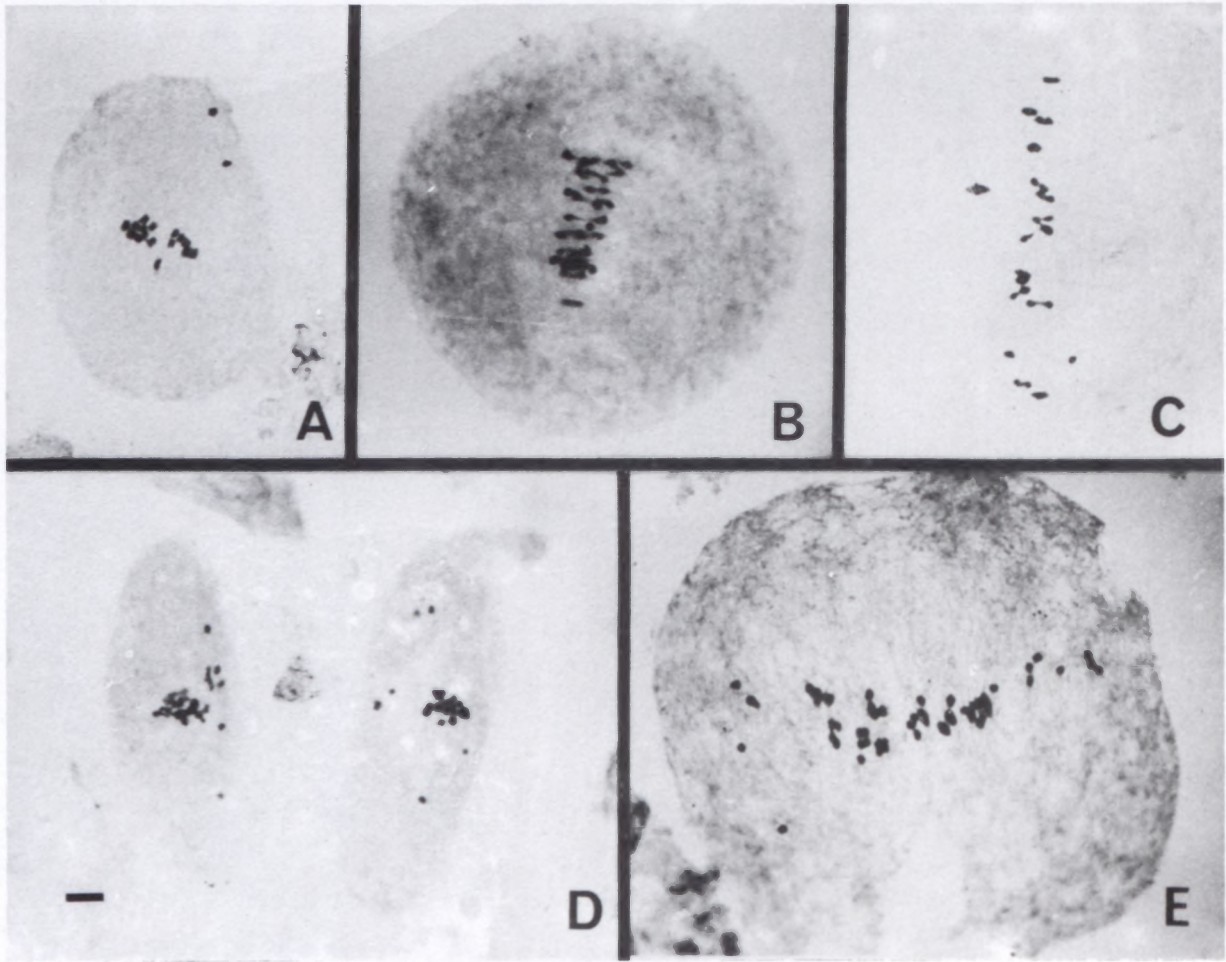


FIGURE 2.—Variation in number of univalents observed during metaphase I and II in *Cenchrus ciliaris*. A, *Spies* 5883, $n = 17$, two univalents; B, *Spies* 5508, $n = 2x = 18$, one univalent; C, *Spies* 5543, $n = 2x = 18$, two univalents; D, *Spies* 5210, $n = 5/2x = 45/2$, five univalents in each cell; E, *Spies* 5514, $n = 3x = 27$, eight univalents. Scale bar: 10 μm .

Chromosome pairing during prophase plays a critical role in the sequence of meiotic events that follow. The success of chromosome pairing during the early stages of the first meiotic division, will affect the viability of the meiotic gametes formed. Incomplete chromosome pairing will lead to various meiotic irregularities, such as the formation of univalents, the presence of chromosome laggards and micronuclei.

The partial or complete loss of chromosome pairing observed during prophase and metaphase I can be attributed to one of two processes, namely asynapsis or desynapsis. Asynapsis (Randolph 1928) is the absence of chromosome pairing during the first meiotic division, whereas desynapsis (Li *et al.* 1945) is the failure to maintain association after first synapsis in prophase. The paired chromosomes, therefore, dissociate during diplotene. The action of asynaptic genes is recognisable when most, or all of the chromosomes, remain as univalents at diakinesis and metaphase I. These genes also induce polyploid meiocytes, elongated and curved spindles, and the misdivision of univalents (Miller 1963). Beadle (1930) assigned the gene symbol 'as' to these types of mutants.

Prakken (1943) classified desynaptic mutants, depending upon their expressivity, into three categories, namely weakly desynaptic (several univalents), intermediate desynaptic (many univalents) and completely desynaptic (exclusively univalents and rarely any bivalents). The cytogenetic results of this study indicate the presence of desynaptic genes. Univalents observed during diplotene and metaphase I were accompanied by bivalents and occasionally quadrivalents (Figure 2C). Not all of the chromosomes present were univalents (Figure 2B, C, E). *Cenchrus ciliaris* is thus an intermediate desynaptic species.

The variation in the number of univalents present in the cells, excludes the presence of asynaptic genes, since asynapsis is associated with complete lack of chromosome pairing. The variation in the number of univalents also varied among the cells of a particular specimen, and among specimens belonging to the same polyploid level. This suggests that within the chromosome complement of a species, there may be differences among the different chromosomes concerning their requirements for the initiation of pairing (Rees 1958; Swaminathan & Murty 1959; Koduru & Rao 1981). Since chiasmata in desynaptic mutant plants are mostly terminal and rarely interstitial at metaphase I (Li *et al.* 1945), the number of rod and ring bivalents were noted particularly during metaphase I. Most of the bivalents observed within the specimens of all three polyploid levels, were linear (Figure 2B, C, E), indicating terminal chiasmata. This observation confirmed the presence of synaptic mutants in this species.

Previous studies indicated that *C. ciliaris* forms an agamic complex and all ploidy levels represent specimens which are allopolyploid or segmental allopolyploid tending towards allopolyploidy (References listed in Visser *et al.* 1998a, b, c). These specimens are consequently supposed to behave meiotically almost as diploids. Although the very low frequency of multivalents formed in a few

specimens could contribute to the formation of univalents, we regard that contribution as insignificantly low and consider the majority of univalents in this study as the result of desynaptic genes.

Spontaneous synaptic mutants exhibit monogenic recessive inheritance mostly (Koduru & Rao 1981) and have been isolated from natural populations. The majority of synaptic mutants reported in the higher plants have been identified in diploid species, such as *Hordeum vulgare* L. (Ramage 1985). Fifteen desynaptic genes have been identified in barley, of which 13 were of spontaneous origin and two were induced (Hernandez-Soriano *et al.* 1973; Hernandez-Soriano & Ramage 1974, 1975).

Chromosome behaviour during anaphase I differed among the various specimens studied. Univalents lying away from the spindle equator during metaphase I, were randomly distributed as laggards to the poles during anaphase I. Univalents distributed on the metaphase plate orientated themselves axially and divided into chromatids, which in turn lagged during segregation to opposite poles during anaphase I (Figure 3A–I). This precocious disjunction of chromosomes into chromatids during anaphase I, was observed in 24 of the specimens studied (Table 1). These specimens represented all three polyploid levels (Figure 3A–I) (Table 1). The number of chromosomes participating in the precocious disjunction varied from one to a maximum of 15 (Table 1).

The premature segregation of some univalents into chromatids resulted, in the case of a tetraploid specimen ($n = 2x = 18$) with two univalents, in a 20/20 distribution of chromosomes and chromatids during late anaphase I. In a normal cell, an 18/18-chromosome distribution is expected. The segregating chromatids were, due to their smaller size, distinguished from the normal chromosomes (Figure 3A–E). The segregating chromosomes were organised into dyad nuclei, whereas the chromosome and/or chromatid laggards were included in micronuclei.

Temperature, humidity and chemicals (Prakken 1943; Ahloowalia 1969; Koduru & Rao 1981) may influence the degree of chromosome pairing in synaptic mutants. It also varies from plant to plant, day to day, year to year and between specimens collected at different times during the same day (Prakken 1943; Soost 1951). The degree of expression of each synaptic gene is also variable. Goodspeed & Avery (1939) reported, with regard to an asynaptic mutant of *Nicotiana sylvestris* L., that high temperature and low humidity greatly increased asynapsis, whereas high temperatures and high humidity decreased asynapsis. Ahloowalia (1969) recorded, in a desynaptic mutant of *Hordeum vulgare* ($2n = 14$), that at lower temperatures (11°C), the mean number of bivalents/cell was 7.71, but that at 28°C, the mean number of bivalents dropped to 5.39 bivalents/cell due to desynapsis. In contrast, Li *et al.* (1945) observed a greater degree of pairing at higher temperatures and decreased pairing at lower temperatures in desynaptic mutants of *Triticum aestivum* L.

The *Cenchrus ciliaris* specimens studied, were collected in areas with a very low average annual rainfall.

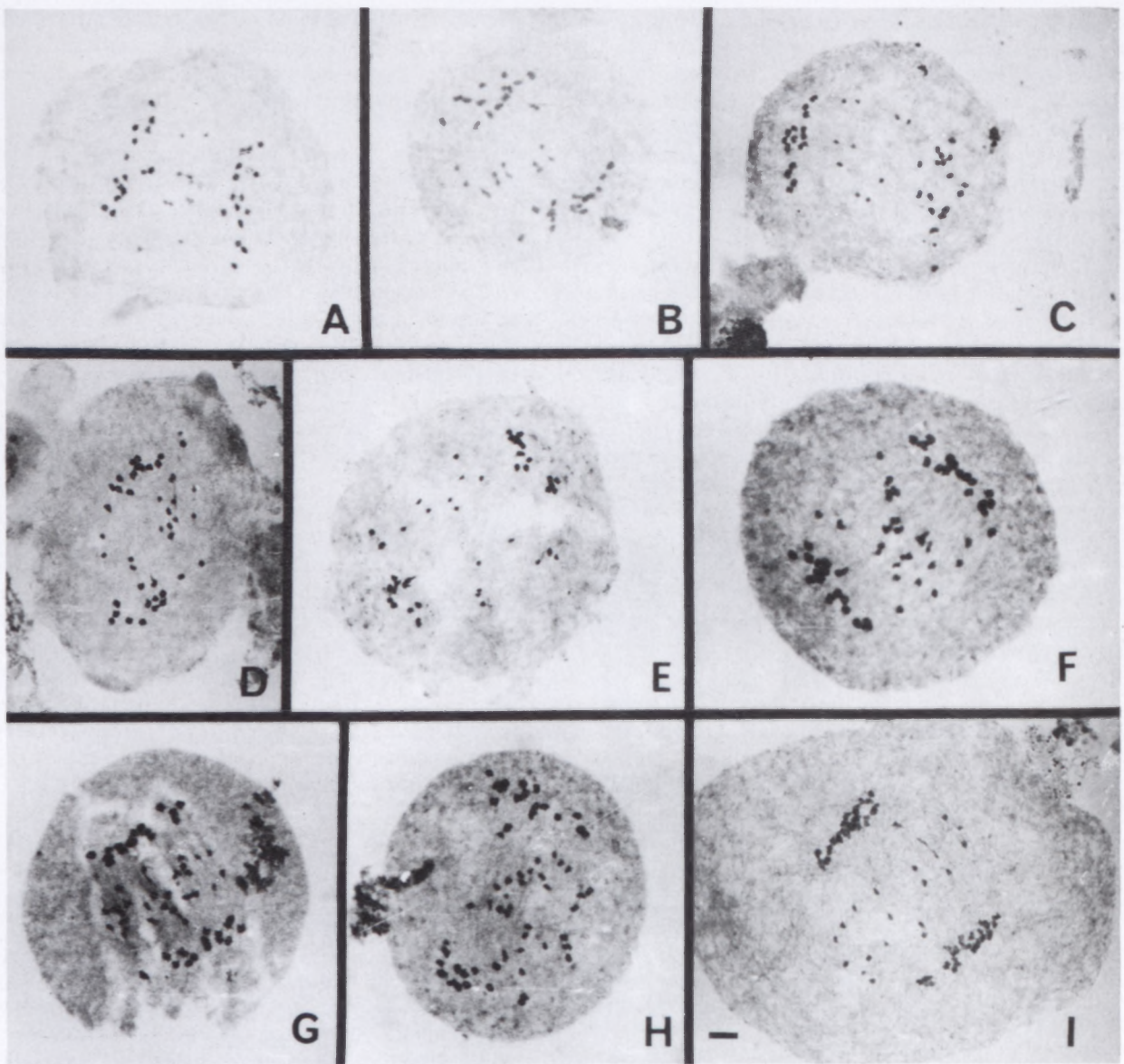


FIGURE 3.—Variation in the number of chromosomes undergoing precocious disjunction during anaphase I in *Cenchrus ciliaris*. A, *Spies 5531* & B, *Spies 5512*, $n = 2x = 18$, 15-15 chromosome distribution, with six chromosome laggards segregating into chromatids; C, *Spies 5230*, $n = 2x = 18$, 15-16 chromosome distribution, with five laggards segregating into chromatids; D, *Spies 5231*, $n = 2x = 18$, 14-14 chromosome distribution, with three segregating laggards; E, *Spies 5240*, $n = 2x = 18$, 13-15 chromosome distribution, with eight laggards; F, *Spies 5583*, $n = 5/2x = 45/2$, 16-17 chromosome distribution, with approximately nine laggards; G, H, *Spies 5581*, $n = 5/2x = 45/2$, various chromosomes and chromatids lagging; I, *Spies 5517*, $n = 3x = 27$, with a minimum of nine laggards segregating into chromatids during anaphase I. Scale bar: 10 μ m.

These areas represent some of the hottest and least humid geographical regions in South Africa. Therefore, the geographical distribution and environmental factors could also have had an influence on the desynapsis observed within specimens belonging to this species.

The disjunction of the chromosomes during anaphase I in *C. ciliaris* was not normal according to the description of meiotic behaviour for desynaptic mutants previously mentioned. Very few chromosome laggards observed during anaphase I, did not undergo disjunction into chromatids (Figure 3A–E). This chromosome abnormality was representative of all three polyploid levels and was observed in 47.7% of all the specimens studied (Table 1). The high percentage of precocious disjunction suggests the presence of a mutated gene responsible for the disjunction of chromosomes.

A meiotic mutant that shows precocious centromere division, 'pc', in *Lycopersicon esculentum* Mill. was described by Clayberg (1959). Chromosome pairing was normal until metaphase I. The precocity first appeared at anaphase I in some bivalents that often lagged and underwent premature centromere division. The centromeres of those chromosomes not lagging during the first division, divided mostly during prophase II. All of these chromosomes were regularly oriented on the metaphase II plate. The precociously divided chromosomes moved at random to the poles without further division. Many chromosomes lagged in the second division and frequently formed restitution nuclei. The mutation segregates as a single recessive gene, 'pc'.

Although in *Cenchrus ciliaris* the situation differs to some extent, chromosome pairing was mostly normal

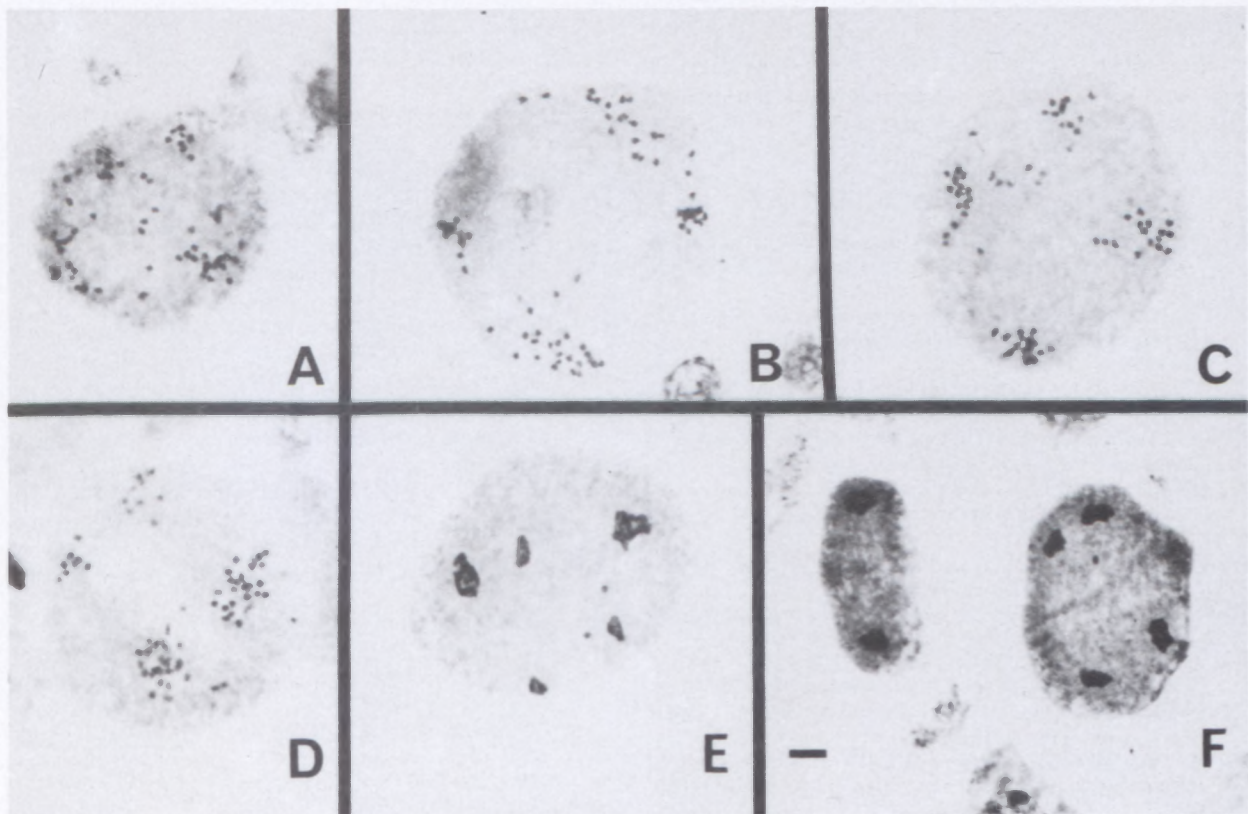


FIGURE 4.—Absence of cytokinesis in *Spies 5512*, resulting in four-nucleated cells. A, anaphase I, ~65 chromosomes; B, anaphase I, ~70 chromosomes; C, anaphase I, ~66 chromosomes; D, anaphase I, ~68 chromosomes; E, telophase I, one nucleus in each pole, with three micronuclei; F, telophase II, normal-sized telophase II cell, with abnormal telophase II cell (four nuclei and one micronucleus). Scale bar: 10 μ m.

until metaphase I. The precocity first appeared at anaphase I in some chromosomes that lagged and underwent premature centromere division. The presence of a gene responsible for precocious centromere division, could, therefore, also be functional in this species.

One specimen, *Spies 5512* ($n = 2x = 18$), exhibited normal chromosome behaviour until telophase I, but cytokinesis did not occur in some of the meiocytes studied (Figure 4A–F). Two spindles formed in some of the cells, resulting in four anaphase I poles (Figure 4A–D). This resulted in cells containing a total of approximately 62 to 69 chromosomes, being distributed amongst the four poles during anaphase I. The lack of cytokinesis resulted in gametes with unequal chromosome constitutions. Chromosomes not segregating to the nearest pole were excluded from the main nuclei, and included in additional micronuclei (Figure 4E, F). Another chromosome disjunction mutant, namely the recessive mutant ‘*va*’, may be active in this specimen. Beadle (1932) first identified this mutant in maize. He based his hypothesis on the fact that a homozygous plant (*va/va*) exhibited a normal prophase I, but cytokinesis was absent during telophase I. This resulted in gametes with diploid and tetraploid chromosome constitutions (Singh 1993). Beadle (1932) stated that failure of cytokinesis might either occur at the first or the second meiotic division. Due to the lack of cytokinesis, an increase in chromosome numbers can occur. This mutant gene could, therefore, be the reason for higher polyploid levels within this species.

Due to the lack of cytokinesis in some of the cells belonging to this specimen, the disjunction gene, ‘*va*’,

may be present. Since this specimen was collected near the only hexaploid ($n = 3x = 27$) specimens studied (*Spies 5514*, *5515* & *5517*), this mutated gene could have been responsible for the high polyploid levels in this area.

CONCLUSIONS

The cytogenetic results indicate the presence of synaptic mutants in *C. ciliaris*. This statement is based on incomplete chromosome pairing, which led to the origin of various chromosome irregularities observed during meiosis. This species was characterised as an intermediate desynaptic species. Geographical distribution and environmental factors, such as high temperatures and low humidity, could also have had an additional influence on the desynapsis observed in this species.

The disjunction of chromosomes during anaphase I was mostly abnormal in this desynaptic species. Precocious disjunction of chromosomes during anaphase I led to the formation of chromatids. Due to the high incidence of this chromosome abnormality, a mutant gene, ‘*pc*’, responsible for the disjunction of chromosomes, may be present. The lack of cytokinesis in one specimen indicates the possible presence of a recessive mutant gene, ‘*va*’ in this species.

It is, therefore, concluded that three meiotic mutant genes could be active in this species, namely the desynaptic mutant ‘*as*’, active during prophase, and the two chromosome disjunction mutant genes ‘*pc*’ and ‘*va*’.

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