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The 'A' genome donor of *Eleusine coracana* (L.) Gaertn. (Gramineae)

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Summary. In an attempt to discover 'A' and 'B' genome donor(s) to finger millet, *Eleusine coracana*, or its progenitor species, *E. africana* (both allotetraploid 2n = 4x = 36), five diploid species, *E. indica*, *E. floccifolia*, *E. multiflora*, *E. tristachya* and *E. intermedia*, were crossed to finger millet and its progenitor taxon. Crosses were successful only with *E. coracana*. Three combinations of triploid hybrids *E. coracana* × *E. indica*, *E. coracana* × *E. floccifolia*, and *E. coracana* × *E. multiflora* were obtained and analysed. Meiotic behaviour was perfectly normal in parental species. The regular number of 18 bivalents in *E. coracana*, 9 bivalents in *E. indica*, *E. intermedia*, *E. tristachya* and *E. floccifolia* and 8 bivalents in *E. multiflora* were invariably noticed. In *E. coracana* × *E. indica* hybrids a mean chromosome pairing of $8.84_{I}+8.80_{II}+0.03_{III}+0.10_{IV}$ per cell was found. About 86.5% of the cells showed the typical $9_{I}+9_{II}$ configuration, suggesting that *E. indica* (AA) is one of the diploid genome donors to cultivated species *E. coracana*. A mean chromosome pairing of $11.08_{I}+7.63_{II}+0.16_{III}+0.04_{IV}$ per cell was found in *E. coracana* × *E. floccifolia* hybrids. Two to ten bivalents and varying numbers of univalents were seen in 55% of the cells. About 45% of the cells showed the $9_{I}+9_{II}$ configuration. Various evidence suggests that perennial *E. floccifolia* is a primitive member of the 'A' genome group of *Eleusine* species, and it may not be a genome donor to *E. coracana*. In *E. coracana* × *E. multiflora* hybrids (2n = 26) mean chromosome pairing of $21.45_{I}+1.97_{II}+0.13_{III}+0.04_{IV}$ per cell was found. About 91% of the cells were observed to have 20–26 univalents. Only a small percentage of the cells contained bivalents or multivalents. This pairing behaviour indicates that *E. multiflora* lacks genomic homology with the 'A' or 'B' genome of *E. coracana*. Genomically *E. multiflora* is a distinct species and a genomic symbol of 'C' is assigned to it. Identification of the 'B' genome donor species to cultivated millet. *E. coracana* remains elusive.

Key words: *Eleusine coracana* – Finger millet – Polyploidy – Interspecific hybrids – Genome analysis

Introduction

Eleusine Gaertn. is a predominantly African genus with nine to ten species, one of these being *Eleusine coracana* (L.) Gaertn., commonly known as finger millet, an important cereal crop that is widely cultivated in southern and eastern parts of Africa and South Asia (Phillips 1972). This genus includes diploid and tetraploid species with three basic chromosome numbers: eight, nine and ten. Among the diploids the basic chromosome number is eight in *E. multiflora* (2n = 2x = 16), nine in *E. indica*, *E. tristachya*, *E. floccifolia* and *E. intermedia* (all 2n = 2x = 18) and ten in *E. jaegeri* (2n = 2x = 20). Tetraploids *E. coracana* and *E. africana* have a basic chromosome number of nine (2n = 4x = 36) (Hiremath and Chennaveeraiah 1982; Salimath 1990). Based on various lines of evidence Chennaveeraiah and Hiremath (1991) proposed that the original basic number of chromosomes for this genus is nine and that other base numbers are derived from dysploid changes therein. *E. coracana* and *E. africana* regularly show the formation of 18 bivalents during meiosis, and apparently these two taxa are allotetraploid in origin (Hiremath and Chennaveeraiah 1982). From chromosome pairing data on an *E. coracana* × *E. africana* hybrid Chennaveeraiah and Hiremath

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(1974a) showed that the genomes of these two species are fully homologous. They further suggested the direct origin of *E. coracana* from *E. africana* through selection and further cultivation of a large grain mutant. A genomic notation of AABB has been assigned to these two species. Thus, allopolyploidy has played a significant role in the origin and evolution of finger millet and its wild progenitor (Hiremath and Chennaveeraiah 1982).

Chennaveeraiah and Hiremath (1974a) also attempted to identify the diploid 'A' and 'B' genome donor of cultivated species *E. coracana*. In an *E. coracana* × *E. indica* triploid hybrid they found only 27 univalents. From this chromosome pairing data they suggested that *E. indica* may not be the 'A' genome donor of *E. coracana* or *E. africana*. However, they cautioned about their conclusion as the chromosome pairing data was from a single hybrid based on 45 cells only. Genus *Eleusine* includes five diploid taxa, and it is still unclear which of the diploid species are the 'A' and 'B' genome donor to *E. coracana* and *E. africana*. In an attempt to identify the 'A' and 'B' genome donors to this millet the diploid species *E. indica*, *E. floccifolia*, *E. multiflora*, *E. tristachya* and *E. intermedia* were crossed with both *E. coracana* and *E. africana*. Only triploid hybrids with *E. coracana* reached maturity, and we subsequently analysed chromosome pairing behaviour in these triploid hybrids. The present paper deals with the 'A' genome donor of *E. coracana*.

Materials and methods

Seed material of different *Eleusine* species was obtained from various germ plasm banks, individual botanists and research organizations. In *Eleusine* species the inflorescence consists of digitately arranged spikes in a terminal umbel form. Each spikelet normally contains four to eight florets, rarely up to ten. The florets are hermaphrodite with three stamens and a bifid feathery stigma. Crossing experiments were carried out in open field with potted plants. The emasculation technique is tedious because of the small size of the florets and their compact arrangement. Crosses were successful only when *E. coracana* was used as a pistil parent. The florets were hand emasculated basically according to the technique of Richardson (1958) with suitable modifications. The number of florets emasculated and pollinated in each cross, the number of F_1 hybrid seeds obtained, the number of F_1 hybrid seedlings reaching maturity and the percentage of crossability are presented in Table 1. Genetic marker characters were used to identify the hybrid seedlings; confirmation was carried out later by cytological means.

For meiotic analysis the young spikes were fixed in Carnoy's fluid (6:3:1), and the PMCs were stained with 2% acetocarmine. The slides were permanently fixed using Celariar's (1956) butyl alcohol schedule and mounted in euparal. Pollen fertility in the species tested and their hybrids was determined on the basis of the stainability of pollen grains in 1:1 acetocarmine glycerine mixture. The morphological comparison of quantitative characters in the parents and hybrids is based on metroglyph analysis of *Eleusine* species by Chennaveeraiah and Hiremath (1974b).

Results

Morphology

E. coracana, *E. indica*, *E. floccifolia*, *E. tristachya*, *E. multiflora* and *E. intermedia* are morphologically distinct species and true to their species descriptions. Comparative accounts of the morphological characters of the parents and their F_1 hybrids, i.e. *E. coracana* × *E. indica*, *E. coracana* × *E. floccifolia*, *E. coracana* × *E. multiflora* and *E. coracana* × *E. tristachya*, are shown in Tables 2–5 and Fig. 1a–i.

Meiotic behaviour

Meiotic behaviour in the tetraploid female parent *E. coracana* was absolutely normal: a normal 18 bivalents were noted at diakinesis and metaphase I in all of the collections of *E. coracana* studied. The diploid taxa *E. indica*, *E. tristachya*, *E. intermedia* and *E. floccifolia* also showed an apparently normal meiosis with 9 bivalents at diakinesis and metaphase I. In *E. multiflora* meiosis was apparently normal with 8 bivalents at diakinesis and metaphase I (Fig. 2a–i).

The F_1 hybrids of *E. coracana* × *E. indica*, *E. coracana* × *E. floccifolia* and *E. coracana* × *E. tristachya* were triploid with 27 chromosomes in their somatic cells. *E. coracana* (n=18) × *E. multiflora* (n=8) F_1 hybrids were also triploids but with 26 chromosomes in their somatic cells. In the hybrids the content of the anthers was poor, therefore it was only with great difficulty that large numbers of cells at diakinesis, metaphase I and other subsequent stages were obtained.

In *E. coracana* × *E. indica* F_1 hybrids a mean chromosome pairing of $8.84_{I}+8.80_{II}+0.03_{III}+0.10_{IV}$ per cell was found in the 178 cells analysed (Table 6). About 154 cells (86.5%) showed a typical $9_{I}+9_{II}$ configuration (Fig. 2f). A single trivalent was seen in 5 cells (Fig. 2h); about 20 cells contained a single quadrivalent (Fig. 2g). One to several laggards were seen in all the anaphase I and II cells examined. All the tetrads examined showed one to many micronuclei.

E. coracana × *E. floccifolia* F_1 perennial hybrids showed a mean chromosome pairing of $11.08_{I}+7.63_{II}+0.16_{III}+0.04_{IV}$ per cell out of the 74 PMCs analysed (Table 6). Nearly 45% of the cells showed a typical $9_{I}+9_{II}$ configuration (Fig. 2i), with the number of bivalents ranging from 2 to 10. Multivalent formation was observed in nearly 15% of the PMCs (Fig. 2j,k): one quadrivalent and 1–2 trivalents were noticed. All of the

Fig. 1a–i. Morphology of spikes of parents and F_1 hybrids. **a** spike of *E. coracana*, **b** spike of *E. indica*, **c** spike of *E. floccifolia*, **d** spike of *E. multiflora*, **e** spike of *E. tristachya*, **f** spike of *E. coracana* × *E. indica* F_1 hybrid, **g** spike of *E. coracana* × *E. multiflora* F_1 hybrid, **h** spike of *E. coracana* × *E. floccifolia* F_1 hybrid, **i** potted plant of *E. coracana* × *E. tristachya* F_1 hybrid

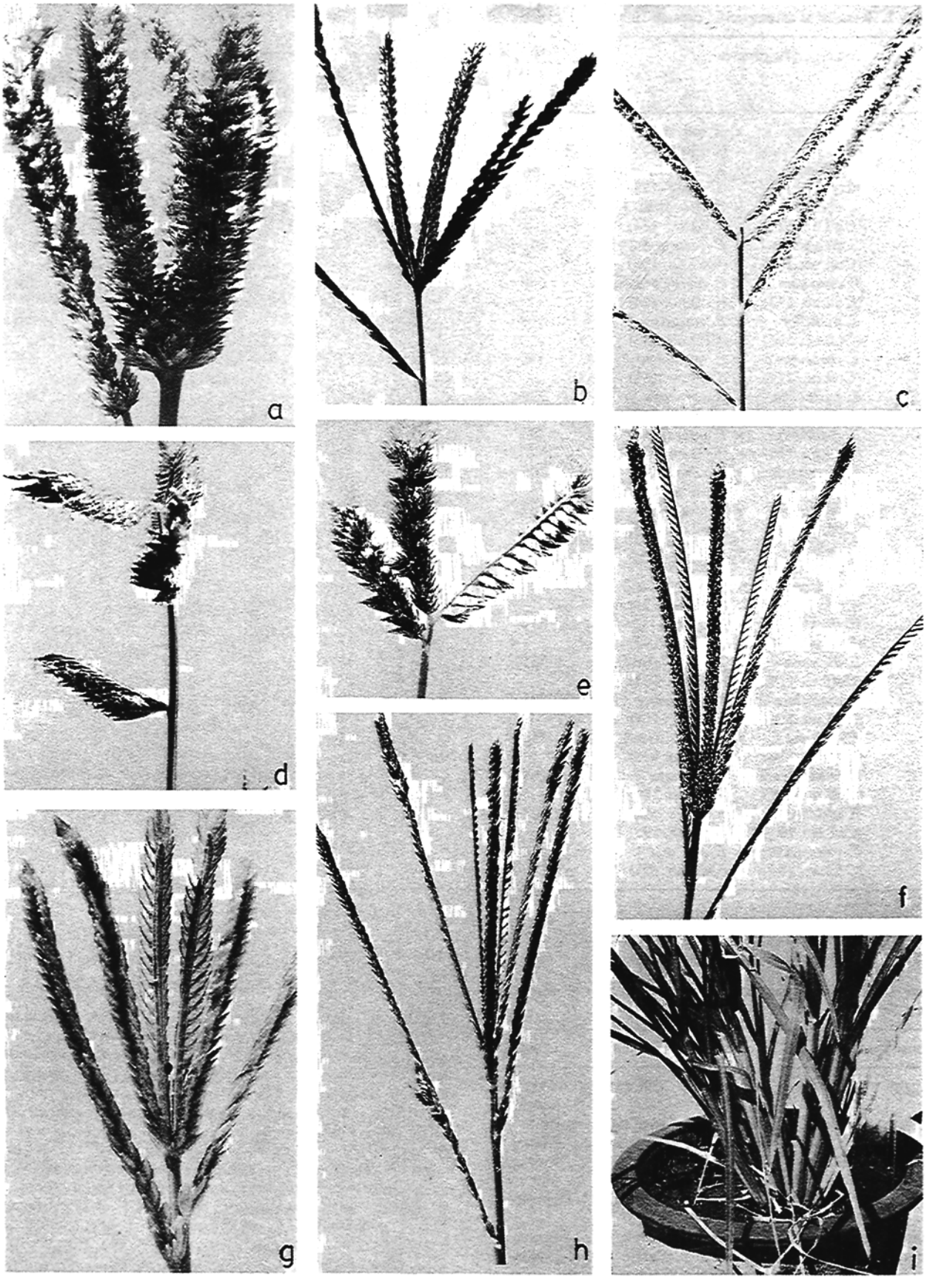
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Table 1. Results of interspecific crosses in *Eleusine* species

Serial/ No.	Interspecific crosses	Number of florets pollinated	Number of F_1 hybrid seeds obtained	Number of F_1 hybrid seeds germinated	Number of seedlings reached to maturity	% of cross-ability
1.	*E. coracana* ♀ (Coll.no. 123) × *E. indica* ♂ (Coll.no. 115)	183	6	4	3	3.3
2.	*E. indica* ♀ (Coll.no. 115) × *E. coracana* ♂ (Coll.no. 123)	194	0	–	–	0.0
3.	*E. coracana* ♀ (Coll.no. 126) × *E. floccifolia* ♂ (Coll.no. 154)	370	19	11	5	5.1
4.	*E. floccifolia* ♀ (Coll.no. 154) × *E. coracana* ♂ (Coll.no. 126)	210	0	–	–	0.0
5.	*E. coracana* ♀ (Coll.no. 133) × *E. multiflora* ♂ (Coll.no. 164)	650	17	17	6	2.6
6.	*E. multiflora* ♀ (Coll.no. 164) × *E. coracana* ♂ (Coll.no. 133)	138	0	–	–	0.0
7.	*E. coracana* ♀ (Coll.no. 117) × *E. tristachya* ♂ (Coll.no. 168)	179	1	1	1	0.5
8.	*E. tristachya* ♀ (Coll.no. 168) × *E. coracana* ♂ (Coll.no. 117)	290	0	–	–	0.0
9.	*E. coracana* ♀ (Coll.no. 116) × *E. intermedia* ♂ (Coll.no. 195)	198	3	1	–	1.5
10.	*E. intermedia* ♀ (Coll.no. 195) × *E. coracana* ♂ (Coll.no. 116)	109	0	–	–	0.0
11.	*E. africana* ♀ (Coll.no. 197) × *E. indica* ♂ (Coll.no. 113)	383	13	13	–	3.4
12.	*E. indica* ♀ (Coll.no. 113) × *E. africana* ♂ (Coll.no. 197)	105	3	–	–	2.9
13.	*E. africana* ♀ (Coll.no. 197) × *E. floccifolia* ♂ (Coll.no. 154)	495	15	12	–	3.0
14.	*E. floccifolia* ♀ (Coll.no. 154) × *E. africana* ♂ (Coll.no. 197)	211	6	3	–	2.8
15.	*E. africana* ♀ (Coll.no. 114) × *E. multiflora* ♂ (Coll.no. 164)	135	0	–	–	0.0
16.	*E. multiflora* ♀ (Coll.no. 164) × *E. africana* ♂ (Coll.no. 114)	201	0	–	–	0.0
17.	*E. africana* ♀ (Coll.no. 114) × *E. tristachya* ♂ (Coll.no. 168)	114	4	1	–	3.5
18.	*E. tristachya* ♀ (Coll.no. 168) × *E. africana* ♂ (Coll.no. 114)	164	0	–	–	0.0
19.	*E. africana* ♀ (Coll.no. 197) × *E. intermedia* ♂ (Coll.no. 195)	221	8	3	–	3.6
20.	*E. intermedia* ♀ (Coll.no. 195) × *E. africana* ♂ (Coll.no. 197)	136	0	0	–	0.0

Table 2. Morphological characters of *E. coracana*, *E. indica* and their F_1 hybrids

Character	*E. coracana*	F_1 hybrid	*E. indica*
Height	Tall, erect	Tall, erect	Short, suberect
Stem	Thick	Medium	Thin
Rachis	Thick	Medium	Thin
Length of spike	Long	Long	Medium
Width of spike	wide	Narrow	Narrow
Nature of spikelet	Non-shattering	Shattering	Shattering
Colour of style	Colourless	Purple	Purple
Condition of grain	Exposed	Sterile	Enclosed

Fig. 2a–m. Meiosis in parents and F_1 hybrids. **a** diakinesis showing 18_{II} in *E. coracana*, **b** metaphase I showing 9_{II} in *E. indica*, **c** diakinesis showing 9_{II} in *E. floccifolia*, **d** diakinesis showing 9_{II} in *E. tristachya*, **e** diakinesis showing 8_{II} in *E. multiflora*, **f** diakinesis showing 9_I+9_{II} in *E. coracana* × *E. indica* F_1 hybrid, **g** diakinesis showing $9_I+7_{II}+1_{IV}$ in *E. coracana* × *E. indica* F_1 hybrid, **h** diakinesis showing $8_I+6_{II}+1_{III}+1_{IV}$ in *E. coracana* × *E. indica* F_1 hybrid, **i** diakinesis showing 9_I+9_{II} in *E. coracana* × *E. floccifolia* F_1 hybrid, **j** diakinesis showing 11_I+8_{II} in *E. coracana* × *E. floccifolia* F_1 hybrid, **k** metaphase I showing $8_I+8_{II}+1_{III}$ in *E. coracana* × *E. floccifolia* F_1 hybrid, **l** metaphase I showing 24_I+1_{II} in *E. coracana* × *E. multiflora* F_1 hybrid, **m** diakinesis showing $7_I+6_{II}+1_{III}+1_{IV}$ in *E. coracana* × *E. multiflora* F_1 hybrid

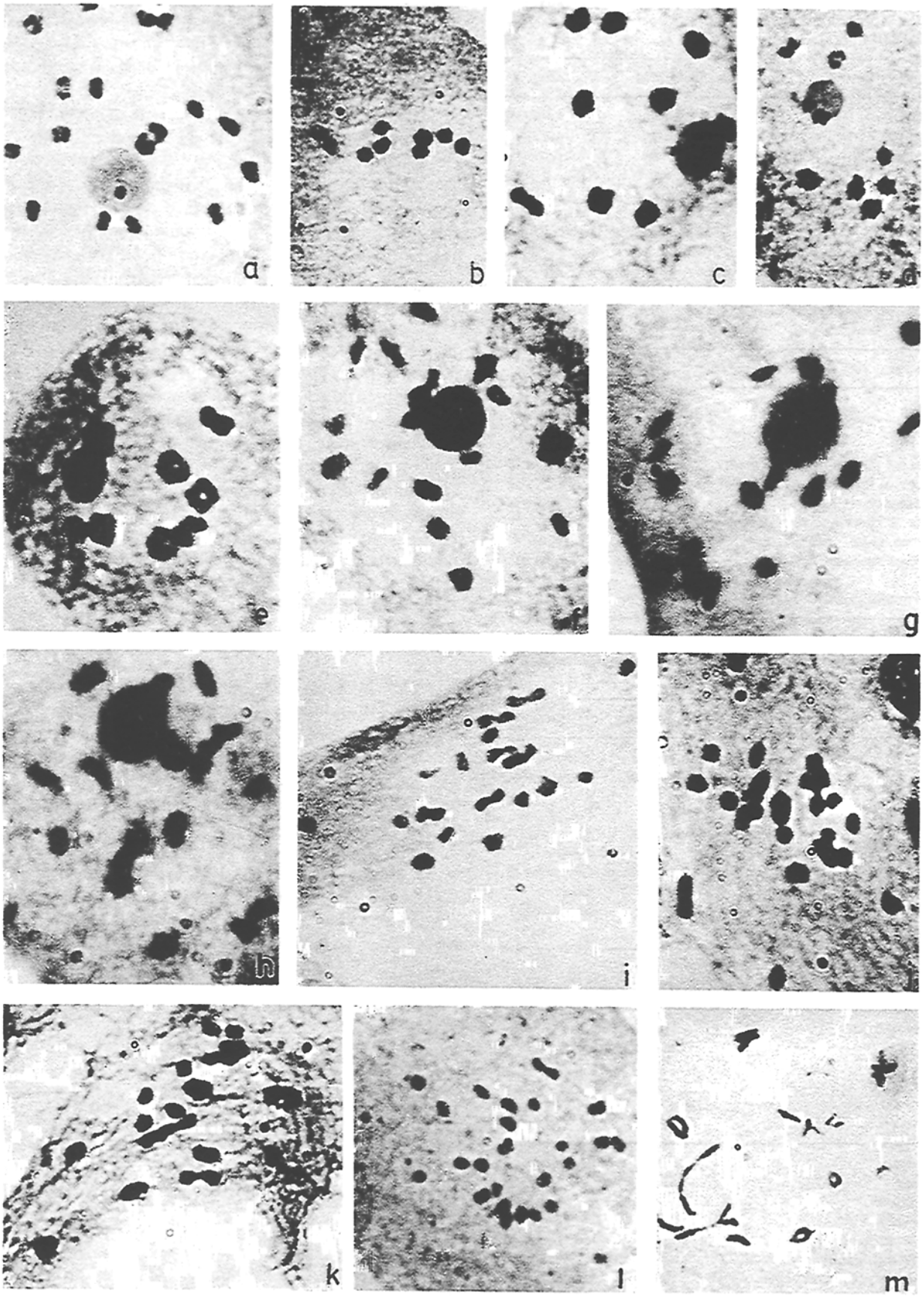
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Table 3. Morphological characters of *E. coracana*, *E. floccifolia* and their F_1 hybrid

Character	*E. coracana*	F_1 hybrid	*E. floccifolia*
Habit	Annual	Perennial	Perennial
Branching	Medium	Profuse	Profuse
Culms	Robust	Medium	Medium
Rachis	Thick	Medium	Thin
Leaf surface	Non-waxy	Waxy	Waxy
Width of spike	Wide	Medium	Narrow
Glumes	Green	Ash coloured	Ash coloured
Condition of grain	Exposed	Sterile	Enclosed

Table 4. Morphological characters of *E. coracana*, *E. multiflora* and their F_1 hybrids

Character	*E. coracana*	F_1 hybrid	*E. multiflora*
Height	Tall	Short	Short
Stem	Thick, erect	Medium, sub-erect	Thin, sub-erect
Pigmentation	Dark green	Green	Pale green
Number of spikes/ inflorescence	Many	More	Few
Length of spike	Long	Medium	Short
Width of spike	Wide	Medium	Narrow
Nature of spikelet	Non-shattering	Shattering	Shattering
Condition of grain	Exposed	Sterile	Enclosed

Table 5. Morphological characters of *E. coracana*, *E. tristachya* and their F_1 hybrids

Character	*E. coracana*	F_1 hybrid	*E. tristachya*
Height	Tall	Medium	Short
Culm	Thick	Medium	Thin
Rachis	Thick	–	Thin
Pigmentation	Purple	Purple	Pale green
Lamina	Long and wide	Medium	Short and narrow
Leaf surface	Hairy-pilose	Hairy-pilose	Glabrous
Length of spike	Long	–	Short
Nature of spikelet	Non-shattering	–	Shattering

150 anaphase I cells and 90 anaphase II cells analysed showed two to several lagging chromosomes. One hundred tetrads were analysed, and all of them contained varying number of micronuclei.

E. coracana × *E. multiflora* F_1 hybrids exhibited highly irregular meiosis. A mean chromosome pairing of $21.45_{I}+1.97_{II}+0.13_{III}+0.04_{IV}$ per cell was found (Table 6), with the number of bivalents ranging from 1 to 8. About 85% of the PMCs contained only 1–3 bivalents and 20–26 univalents (Fig. 21). Only about 29% of the PMCs showed 3–8 bivalents, and 6% of the cells contained all 26 univalents. Five percent of the PMCs showed 1 quadrivalent, and 1–3 trivalents were noticed in 7.8% of the cells examined (Fig. 2m). All 100 anaphase I cells examined contained 1–11 laggards, and varying numbers of laggards were observed in all 82 anaphase II and telophase II cells analysed. Sixty tetrads were analysed, and all of them contained a varying number of micronuclei.

Only one F_1 hybrid seed was recovered from the *E. coracana* × *E. tristachya* cross. This hybrid seed germinated and grew well but did not flower; thus, meiosis in the F_1 hybrid could not be studied. Out of the three hybrid seeds obtained between *E. coracana* × *E. intermedia* only one germinated, and it could not be studied as the hybrid failed to reach maturity.

Fertility

Pollen fertility in all of the collections of *E. coracana* was about 99.9% and seed set was 99%. In both *E. indica* and *E. tristachya* pollen fertility as well as seed set were 99%. *E. multiflora* exhibited 99.5% pollen fertility but only 70% seed setting. In *E. floccifolia* 95% of the pollen was assessed as being good, but it showed only about 45% seed setting.

All of the triploid hybrids produced in the present study, except for the *E. coracana* × *E. tristachya* and *E. coracana* × *E. intermedia* hybrids, grew luxuriantly and flowered well. Anthers were poor in content, and the pollen grains were shrivelled. No pollen was assessed as

Table 6. Chromosome pairing in four *Eleusine* species and their F_1 hybrids

Species/hybrid	Number of cells observed	Chromosome configuration			
		I	II	III	IV
		Average (range)	Average (range)	Average (range)	Average (range)
E. coracana	306	0	18.00 (–)	0	0
E. indica	216	0	9.00 (–)	0	0
E. floccifolia	183	0.04 (0–2)	8.97 (8–9)	0	0
E. multiflora	290	0	8.00 (–)	0	0
E. coracana × *E. indica*	178	8.84 (6–11)	8.80 (6–9)	0.03 (0–1)	0.10 (0–1)
E. coracana × *E. floccifolia*	74	11.08 (6–27)	7.63 (0–10)	0.16 (0–2)	0.04 (0–1)
E. coracana × *E. multiflora*	102	21.45 (5–26)	1.97 (0–8)	0.13 (0–3)	0.04 (0–1)

being good, and all of the triploid hybrids were completely seed sterile.

Discussion

A knowledge of the genome structure of cultivated plants and their wild relatives is essential for any sound plant improvement programme. The basic chromosome number with attendant genes is known as the genome (Jackson 1985). Among angiosperms nearly 70% of the taxa possess more than two genomes and are polyploids (Gottschalk 1985). The establishment of the phylogenetic relationships and origin of polyploid species from their related species and progenitors with a lower genome number is known as genome analysis.

The classical method of genome analysis is observing the degree of chromosome pairing in the meiosis of interspecific F_1 hybrids (Kihara 1930). The formation of bivalents indicates genetic homology between two genomes; the lack of pairing is considered to indicate a lack of genetic affinity. The precise nature of the specificity of this pairing is not well known. This method of genome analysis has its limitations. Chromosome pairing is under genetic control as evidenced by the *Ph* gene in bread wheat (Riley and Chapman 1958). It may also be affected by environmental factors (Solbrig 1968), and several mutant genes are known to affect the meiotic process (Kaul and Murthy 1985; Gottschalk 1987). Finally, genome analysis is possible only when two taxa can be hybridized, and viable hybrids made available for analysis. Despite these limitations Kihara's classical method of genome analysis is considered to be the best one available for elucidating genome relations and the origin of polyploid species (Kimber et al. 1981; Jauhar and Crane 1989; Wang 1989).

Information regarding genome relations in *Eleusine* species is limited. Chennaveeraiah and Hiremath (1974a) showed for the first time that *E. coracana* and *E. africana* are allotetraploid species. They also established that *E. africana* is the wild progenitor of *E. coracana* and that the genomes of these two taxa are identical with a genomic notation of AABB. The progenitor species *E. africana* must have originated from a cross between two diploid taxa having 'A' and 'B' genomes followed by chromosome doubling. If the putative diploid progenitor species with the 'A' or 'B' genome are crossed to *E. africana* (AABB) or *E. coracana* (AABB) then one can expect 9_I+9_{II} configurations in their F_1 hybrids (AAB or ABB). However, if the diploid species is not a genome donor to the tetraploid *E. africana* or *E. coracana*, only 27 univalents would be found in the triploid hybrid (ABC). On this theoretical assumption five diploid species of *Eleusine*, namely *E. indica*, *E. floccifolia*, *E. tristachya* and *E. intermedia* (all n=9) and *E. multiflora* (n=8), were crossed to *E. africana* and *E. coracana*.

Three triploid *E. coracana* × *E. indica* hybrids were produced and analysed. About 86.5% of the cells showed the typical 9_I+9_{II} configuration. This pairing behaviour suggests that *E. indica* (AA) is one of the diploid genome donors to cultivated species *E. coracana* (AABB). A small percentage of cells revealed the presence of trivalents and quadrivalents in addition to bivalents. This is perhaps due to chromosomal interchanges or homoeologous pairing between 'A' and 'B' genome chromosomes. Cytogenetic data from the present study contradict the findings of Chennaveeraiah and Hiremath (1974a): 27 univalents were found in 99.5% of the PMCs in the *E. coracana* × *E. indica* hybrid, which suggests that *E. indica* is unlikely to be a genome donor to *E. coracana*. These results are supported by the work of Hilu (1988) who by means of restriction endonuclease analysis of chloroplast DNA, arrived at the conclusion that *E. indica* is the maternal genome donor to the tetraploid species. One possible reason for the difference between our cytogenetic data and that of Chennaveeraiah and Hiremath (1974a) could be that the latter observed 45 cells from only a single hybrid. At the time they preached caution about their conclusion on this account. Present cytogenetic data is based on three hybrid plants and involves a large number of PMCs and when coupled with morphological data suggests that *E. indica* may be the 'A' genome donor of cultivated finger millet *E. coracana*.

In *E. coracana* × *E. floccifolia* triploid hybrids about 45% of the PMCs revealed the typical 9_I+9_{II} configuration; the remaining 55% of the PMCs reveal 2–8 bivalents and a varying number of univalents. These results suggests that one of the genomes of *E. coracana* is partially homologous with the diploid *E. floccifolia* genome. Does the *E. floccifolia* genome represent the 'A' or 'B' genome? Salimath (1990) observed that *E. indica* × *E. floccifolia* diploid hybrids revealed a regular nine bivalent formation in 80% of the PMCs, thus suggesting that the 'A' genome of *E. indica* is partially homologous with the *E. floccifolia* genome. Apparently *E. floccifolia* is a member of the 'A' genome group of diploid Eleusines, and its genome can be designated as 'Af'. Morphologically *E. floccifolia* is quite different from *E. coracana* and occupies a mountainous grassland habitat. It is unlikely that *E. floccifolia* could be the 'A' genome donor of cultivated *E. coracana*.

E. multiflora (2n=2x=16) is the only diploid species in *Eleusine* with a base number x=8. In *E. coracana* × *E. multiflora* triploid hybrids (2n=26) only a very small percentage of the cells contained bivalents or multivalents. This suggests that *E. multiflora* lacks genomic homology with the 'A' or 'B' genome of *E. coracana* or *E. africana*. The occurrence of a few bivalents or multivalents, however, may indicate an ancestral genomic homology from which all the Eleusines are derived. *E. multiflora* does not cross with any of the diploid Eleusines,

and morphologically also it is distinct from the rest of the diploid species. Thus, this taxon is not a member of the 'A' or 'B' genome group of species. Genomically it is a distinct species and a genomic symbol of 'C' is assigned to it.

E. coracana × *E. tristachya* hybrids germinated and grew well but did not flower and dried off without flowering. Thus, due to a lack of chromosome pairing data a conclusive cytogenetic relationship between *E. coracana* and *E. tristachya* could not be established. Maximum growth, development and differentiation of *Eleusine* has taken place in Africa. Geographically *E. tristachya* is distributed in South America, and Africa is not the natural range of its distribution (Phillips 1972). Phytogeographic evidence suggests that *E. tristachya* is unlikely to be the 'B' genome donor of *E. coracana* or *E. africana*. Using restriction site homology of chloroplast DNA, Hilu (1988) showed that *E. tristachya* differs from *E. indica*, *E. coracana* and *E. africana* by at least one mutational event for each restriction enzyme studied. Its genomic relationship with *E. coracana* can be deduced indirectly from diploid × diploid species hybrids involving *E. tristachya*. Chennaveeraiah and Hiremath (1973) deduced from chromosome pairing data on an *E. tristachya* × *E. floccifolia* hybrid that the genomes of these two species are homologous. Further, *E. tristachya* × *E. indica* F_1 hybrids have commonly nine bivalents in 89% of the PMCs (Salimath 1990). The present investigation has shown that *E. indica* is the 'A' genome donor to *E. coracana* and that its 'A' genome is homologous to the genome of *E. floccifolia*. Thus, *E. indica*, *E. tristachya* and *E. floccifolia* belong to the 'AA' genome group of the Eleusines. No conclusion can be drawn regarding the genome affinity of *E. intermedia* as crosses between it and *E. coracana* or any other diploid species were unsuccessful. Among the remaining diploid species, *E. jaegeri* (n = 10) with its different base number, is most unlikely to be the 'B' genome donor because it is a perennial mountainous grass with no morphological resemblance to *E. africana* or *E. coracana*. The 'B' genome donor of *E. coracana* remains elusive. It would be worthwile to look for 'B' genome candidature in the diploid taxa of allied genera.

References

Celariar RP (1956) Tertiary butyl alcohol dehydration of chromosome smears. Stain Technol 31:155–157

Chennaveeraiah MS, Hiremath SC (1973) Genome relationship of *Eleusine tristachya* and *E. floccifolia*. J Cytol Genet 8:1–5

Chennaveeraiah MS, Hiremath SC (1974a) Genome analysis of *Eleusine coracana* (L.) Gaertn. Euphytica 23:489–495

Chennaveeraiah MS, Hiremath SC (1974b) Character association pattern in *Eleusine* Gaertn. Karnatak Univ J Sci 19: 257–275

Chennaveeraiah MS, Hiremath SC (1991) Cytogenetics of minor millets. In: Tsuchiya T, Gupta PK (eds) Chromosome engineering in plants: genetics, breeding and evolution. Elsevier Sci Pub, Amsterdam, The Netherlands, pp 613–627

Gottschalk W (1985) Polyploidy and its role in the evolution of higher plants. In: Sharma AK, Sharma A (eds) Advances in chromosome and cell genetics. Oxford and IBH, New Delhi, pp 1–43

Gottschalk W (1987) III Mutation: higher plants. Prog Bot 49:216–230

Hilu KW (1988) Identification of the "A" genome of finger millet using chloroplast DNA. Genetics 118:163–167

Hiremath SC, Chennaveeraiah MS (1982) Cytogenetical studies in wild and cultivated species of *Eleusine* (Gramineae). Caryologia 35:57–69

Jackson RC (1985) Genomic differentiation and its effect on gene flow. Syst Bot 10:391–404

Jauhar PP, Crane CF (1989) An evaluation of Baum et al.'s assessment of the genomic system of classification in the Triticeae. Am J Bot 76:571–576

Kaul MLH, Murthy TGK (1985) Mutant genes affecting higher plant meiosis. Theor Appl Genet 70:449–466

Kihara H (1930) Genomanalyse bei *Triticum* und *Aegilops*. I. Cytologia 2:106–156

Kimber G, Alonso LC, Sallee PJ (1981) The analysis of meiosis in hybrids. I. Can J Genet Cytol 23:209–213

Phillips SM (1972) A survey of the genus *Eleusine* Gaertn. (Gramineae) in Africa. Kew Bull 27: 251–270

Richardson WL (1958) A technique of emasculating small grass florets. J Genet 18:69–73

Riley R, Chapman V (1958) Genetic control of the cytological diploid behaviour of hexaploid wheat. Nature 183:713–715

Salimath SS (1990) Cytology and genome relations in some species of *Eleusine* and its allies. Ph.D thesis, Karnatak University, Dharwad, India

Solbrig OT (1968) Fertility, sterility and the species problem. In: Heywood VH (ed) Modern methods in plant taxonomy. Academic Press, London pp 77–96

Wang RRC (1989) An assessment of genome analysis based on chromosome pairing in hybrids of perennial Triticeae. Genome 32:179–189