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Genome interrelationship in the genus *Eleusine* (Poaceae) as revealed through heteroploid crosses

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Abstract — Genome interrelationship in the genus *Eleusine* (Poaceae) has always been a matter of considerable interest for plant breeders whose major objective was to attain genetic improvement in *E. coracana* (finger millet), an important crop of Africa and south Asia. *E. coracana* and *E. africana* are the two major amphidiploid species of *Eleusine* with AABB genome (2n=4x=36). In attempt to identify the A and B genome donor species, heteroploid crosses were made involving these two tetraploid species and four diploid species viz. *E. intermdia*, *E. indica*, *E. floccifolia*, *E. tristachya* (all with 2n=2x=18). The resultant F_1 hybrids were investigated for cytomorphological details. Male meiosis studies in pollen mother cells showed regular occurrence of expected 9II+9I at diakinesis/ metaphase I in majority of the cells indicating the existence of complete and/or partial homology among crossing parents. The occurrence of occasional quadrivalents had apparently no bearing on the course of meiosis owing to their scant number. Anaphase I and II were characterized by unequal distribution and micronuclei leading to drastic reduction in pollen stainability (2-8%) and complete seed seterlity. Our observations suggest that *E. indica* with AA genome is the pivotal donor species in the evolution of *E. africana* and *E. coracana* while *E. intermedia* ($A_{im}A_{im}$) and *E. tristachya* (A_tA_t) belong to A genomic group of diploid Eleusines. Further these three species form a close genetic assemblage within the genus *Eleusine*. The assumption that *E.floccifolia* is a definite B genome donor species is now widely accepted while *E. tristachya* might also be a candidate for BB genome is completely ruled out there by leaving the question wide open regarding identity of the other B genome donor species, if any.

Key words: *Eleusine*, genome interrelationship, interspecific hybrids, male meiosis, triploids.

INTRODUCTION

E. coracana, commonly known as finger millet or *ragi* is mainly cultivated in arid and semi-arid regions of Africa and south Asia for its nutritious grains that are high in protein, fat and mineral content as compared to other popular cereal crops like rice and sorghum (Reed 1976; Barbeau and Hilu 1993) *E. coracana*, the third most important millet, is estimated to occupy about 8% of the cultivable area and 11% of the total production of all the millets in the world (Rachie and Peters 1977). In India it is grown in most of the provinces and about 64% of total production comes from Karnataka (Vijayalakshmi and Hills 2003). The grains are usually converted into flour for making chapatis, cakes, puddings and porridge. The crop has high levels of amino acids like methonine and provides a sustaining diet, particularly for people doing hard manual work. In some parts of Africa and India the grains are used for making beer and a liquor called arak (Hilu and de wet 1976). Finger millet has also been reported to have some medicinal properties and is used as a folk remedy for many diseases (Bhatnagar 1952; Watt and Breyer-Brandwijk 1962). To meet the ever increasing demand, especially in developing countries, efforts have been made for the genetic improvement of finger millet through interspecific hybridization, from time to time (Chennaveeraiah and Hiremath 1973; Hiremath and Salimath 1992; Salimath *et al.* 1995). However, such efforts were often impeded by lack of accurate information on genome interrelationship among various diploid and tetraploid species of the genus *Eleusine*.

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The *Eleusine* Gaertn. is a predominantly an African genus comprising both diploid and tetraploid species. Three basic chromosome numbers (x = 8, 9 and 10) are reported for this genus. The representative species of these three basic numbers are *E. multiflora* (x=8; 2n=2x=16), *E. intermdia*, *E. indica*, *E. floccifolia*, *E. tristachya* (x=9; 2n=2x=18) and *E. jaegeri* (x=10; 2n=2x=20). The tetraploid species *E. coracana* and *E. africana* are based on x=9 and both are assigned AABB genome. *E. kigeziensis* is yet another wild tetraploid taxon with a deviant number of 2n=38, which probably has allopolyploid origin involving two diploid species with x=9 and 10. Identification of true diploid progenitor species of *E.coracana* has been addressed by several workers (CHENNAVEERAIAH and HIREMATH 1974a; HIREMATH and CHENNAVERRAIAH 1982; HIREMATH and SALIMATH 1992; BISHT and MUKAI 2001; 2002). However, an authentic information in this regard can be deduced either by performing crosses of allotetraploids viz. *E. coracana* and *E. africana* with the suspected diploid donor species or by performing Genomic *In situ.* Hybridization (GISH) experiments, both of them having their own importance and utility. HIREMATH and SALIMATH (1992) have crossed *E. coracana* and *E. africana* with diploid species *E. indica*, *E. floccifolia*, *E. multiflora*, *E. tristachya*. But hybrids could be produced only in few cross combinations, for which cytomorphological investigations were carried out. However many important cross combinations like *E. tristachya* x *E. coracana*, *E. intermedia* x *E. coracana* remained unexplored for details leading to ambiguity regarding A and B genome donor species of *E. coracana*. There are still many gaps in our understanding of *Eleusine* species and their interrelationships. Therefore a comprehensive interspecific hybridization programme has been designed involving allotetraploid *E. coracana* and *E. africana* with four diploid species. The following is a detailed cytomorphological treatise of parents and F_1 hybrids of five heteroploid cross combinations in the genus *Eleusine*.

MATERIALS AND METHODS

Seeds of various species of *Eleusine* were obtained either from International Live Stock Centre of Africa, Ethiopia and United States Department of Agriculture, USA. Crossing experiments were conducted in open field with potted plants. Florets were hand emasculated according to the technique of RICHARDSON (1958). Four diploid species of *Eleusine* viz. *E. intermedia*, *E. tristachya*, *E. indica* and *E. floccifolia* were crossed with amphidiploids *E. coracana* and *E. africana*. Genetic marker characters were used to identify the hybrid seedlings; confirmation was carried out later by cytological analysis. Morphological data for various attributes was collected and a comparison of quantitative characters of parents and their F_1 hybrids was made on the basis of Anderson's metroglyph analysis of *Eleusine* as proposed by CHENNAVEERAIAH and HIREMATH (1974b) was carried out.

For meiotic observations, spikes of parents and F_1 hybrids were fixed in Carnoy's fluid (6:3:1 ethanol-chloroform-acetic acid) and the pollen mother cells (PMCs) were stained with 2% acetocarmine. For estimation of per cent pollen stainability, the pollen grains were stained in 1:1 glycerine: actocarmine mixture and on average three slides were scored for stainable pollens.

RESULTS

Five heteroploid cross combinations involving six species of *Eleusine* viz. *E. intermedia* x *E. coracana*, *E. tristachya* x *E. coracana*, *E. africana* x *E. indica*, *E. africana* x *E. floccifolia* and *E. intermedia* x *E. africana* have been attempted in the present investigations.

Crossability - The data on various cross combinations attempted, F_1 seeds harvested, number of seedlings survived till maturity and percentage crossability are presented in Table 1. All in all five

Table 1 — Crossability studies in the genus *Eleusine*

Sl. No.	Crosses	No. of florets Pollinated	No. of hybrid seeds Obtained	No. of hybrid seeds germinated	No. of seedlings reached maturity	% crossability
1.	*E. intermedia* x *E. coracana*	120	10	3	2	8.3
2.	*E. tristachya* x *E. coracana*	265	14	5	4	3.2
3.	*E. africana* x *E. indica*	140	8	2	2	5.7
4.	*E. africana* x *E. floccifolia*	220	12	3	2	5.4
5.	*E. intermedia x E. africana*	300	19	2	2	6..3

interspecific hybrids were obtained which were subjected to detailed analysis.

Morphology - E. coracana, *E. africana*, *E. intermedia*, *E. tristachya*, *E. indica* and *E. floccifolia*, are distinct species and conform to their description (see PHILLIPS 1972). Comparative morphological account of parents and their F_1 hybrids is shown in Tables 2-6.

Meiotic analysis - Diploids and tetraploids: *E. indica* and *E. tristachya* (n=9) exhibited normal meiotic behavior with regular occurrence of nine bivalents at diakinesis/metaphase I. However the other two diploid species *E. intermedia* and *E. floccifolia* had shown the presence of univalents, though with very low frequency (Table 7; Figs.1-2) On the other hand the tetraploid species *E. coracana* and *E. africana* (n= 18) which were used ei-

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

Characters	*E. intermedia*	F_1 hybrid	*E. coracana*
Habit	Perennial	Perennail	Annual
Stem width	Thin	Thick	Thick
No. of spikelet/Inflorescence	Many	Few	More
Spike length	Long	Long	Medium
Spike width	Narrow	Broad	Broad
Nature of spikelet	Shattering	-	Non-shattering
Condition of grain	Enclosed	Sterile	Exposed

Table 3 — Morphological characters of *E. tristachya*, *E. coracana* and their F_1 hybrids.

Characters	*E. tristachya*	F_1 hybrid	*E. coracana*
Height	Short	Medium	Tall
Rachis	Thin	Thick	Thick
Pigmentation	Pale green	Purple	Purple
Leaf surface	Glabrous	Hairy pilose	Hairy pilose
Spike length	Short	Long	Long
Lamina	Short and Narrow	Medium	Long and Wide
Color of style	Color less	Purple	Purple
Color of anther	Yellow	Yellow	Purple
Nature of spikelet	Shattering	-	Non-shattering
Condition of grain	Enclosed	Sterile	Exposed

Table 4 — Morphological characters of *E. africana*, *E. indica* and their F_1 hybrids.

Characters	*E. africana*	F_1 hybrid	*E. indica*
Height	Tall	Medium	Short
Stem	Thick	Medium	Thin
No. of spikelet/Inflorescence	Many	Few	More
Spike length	Long	Medium	Short
Color of style	Color less	Purple	Purple
Color of anthers	Yellow	Purple	Purple

Table 5 — Morphological characters of *E. africana*, *E. floccifolia* and their F_1 hybrids.

Characters	*E. africana*	F_1 hybrid	*E. floccifolia*
Habit	Annual	Perennial	Perennial
Stem	Thick	Medium	Thin
Branching	Medium	Profuse	Profuse
Leaf surface	Non-waxy	Waxy	Waxy
Leaf margin	Without hairs	With wooly hairs	With wooly hairs
No. of spikes/ Inflorescence	Many	Few	More
Glumes color	Green	Grey	Grey

Table 6 — Morphological characters of *E. intermedia*, *E. africana* and their F_1 hybrids.

Characters	*E. intermedia*	F_1 hybrid	*E. africana*
Habit	Perennial	Perennial	Annual
Stem width	Thin	Medium	Thick
No. of spikelet/Inflorescence	Many	Few	More
Spike length	Long	Medium	long
Color of style	Color less	Purple	Purple
Color of anthers	Yellow	Purple	Purple

Table 7 — Chromosome associations at diakinesis/ metaphase I of meiosis in *Eleusine* species and their F_1 hybrids.

Species/hybrids	2n	No. of cells analysed	Chromosome Associations								
			Univalents			Bivalents			Quadrivalents		
			No.	Mean	Range	No.	Mean	Range	No	Mean	Range
E. coracana	36	305	-	-	-	5490	18.0	-	-	-	-
E. africana	36	460	-	-	-	8280	18.0	-	-	-	-
E. indica	18	120	-	-	-	1080	9.0	-	-	-	-
E. tristachya	18	145	-	-	-	1305	9.0	-	-	-	-
E. intermedia	18	218	36	0.17	0-2	1929	8.85	8-9	-	-	-
E. floccifolia	18	97	19	0.19	0-2	862	8.89	8-9	-	-	-
E. intermedia x *E. coracana*	27	109	963	8.83	7-9	934	8.56	3-9	28	0.25	0-3
E. tristachya x *E. coracana*	27	119	1099	9.23	7-9	1029	8.65	7-10	14	0.11	0-1
E. africana x. *E. indica*	27	88	738	8.38	5-9	805	9.14	4-11	7	0.08	0-2
E. africana x *E. flocifolia*	27	44	370	8.40	5-9	375	8.52	5-9	17	0.38	0-3
E. intermedia x *E. africana*	27	67	585	8.73	7-9	538	8.03	1-10	37	0.55	0-4

ther as male or female parent in different crosses showed regular occurrence of 18 bivalents at diakinesis and/or metaphase I. (Table 7; Fig. 3)

F1 hybrids: The meiotic data of F_1 hybrids from the five cross combinations has been summarized in Table 7 and illustrated in Figs. 4-11.

The F_1 hybrid of *E. inermedia* x *E. coracana* had shown typical 9II + 9I association in about 78% of 109 PMCs analyzed meiotically. It was further characterized by the presence of occasional quadrivalents which were observed in few cells. On average each cell had 0.25 IV + 8.48 II + 8.75 I (Figs. 4-5). Cells analyzed at anaphase I and II of this hybrid had shown one to many laggards. Micronuclei in varying number were recorded in pollen tetrads.

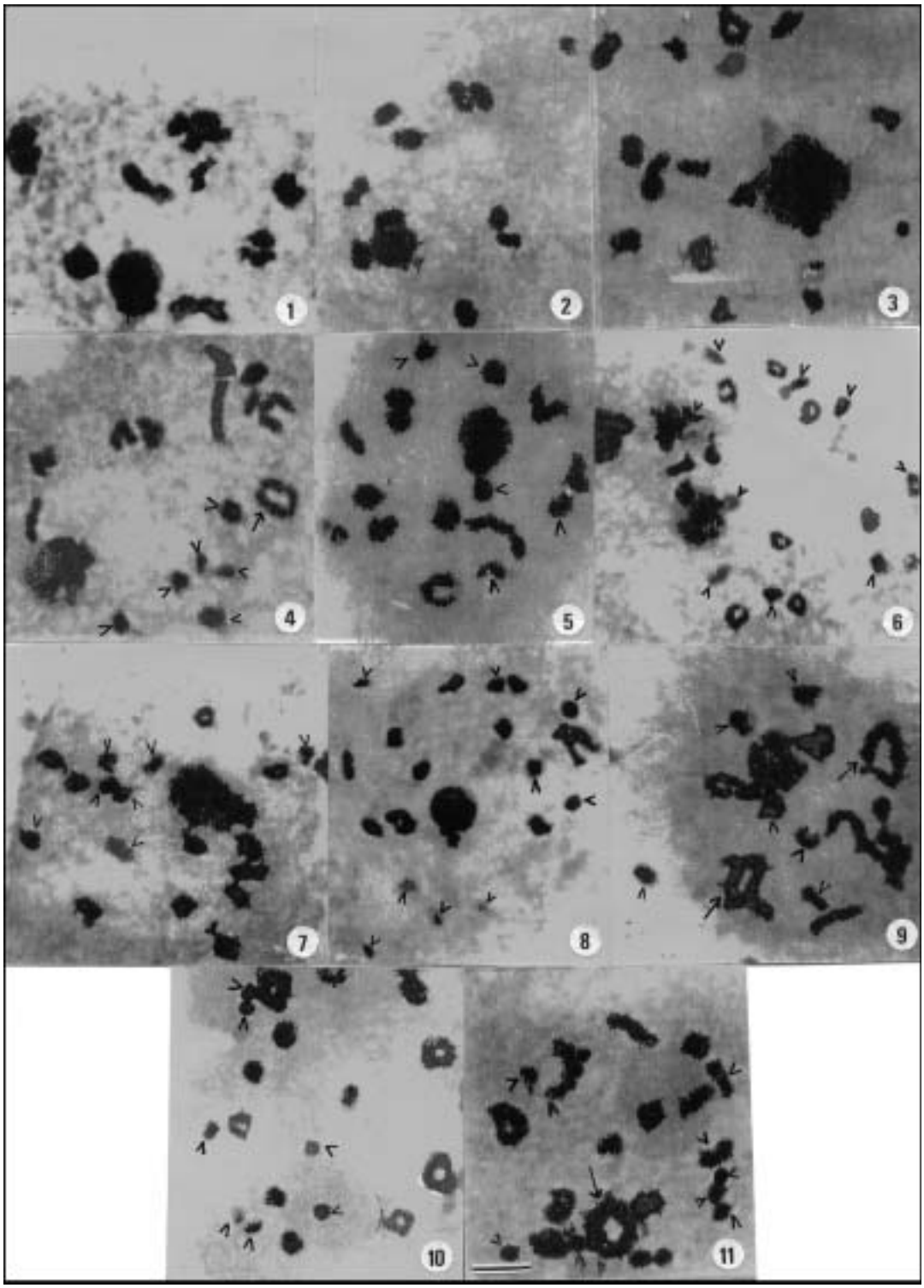
In *E. tristachya* x *E. coracana* cross, the F_1 hybrid showed typical 9II + 9I in 71% of PMCs analyzed, while the remaining had a mixture of univalents, bivalents, and qadrivalents. On average each cell had 0.11 IV + 8.89 II + 9. 39 I. Lagging univalents at anaphase I and micronuclei in the telophase II were observed.

The F_1 of *E. africana* x *E. indica* had 9II + 9I in 74% PMCs analyzed and the remaining cells had a mixture of univalents trivalents and quadrivalents. On average in this hybrid had 0.08 IV + 9.07 II + 8.38 I. (Figs. 6-7). The cells analyzed at AI and AII had unequal distribution of chromosomes and all the quatrets analyzed contained varying number of micronuclei.

In *E. africana* x *E. floccifolia* cross, the F_1 hybrid showed about 72.2% cells with 9II + 9I association. The average number of chromosome association per cell was 0.38 IV + 8.54 II + 8.40 I. (Fig. 9). One to many laggards were noted at anaphase I and II.

The F_1 hybrid of *E. intermedia* x *E. africana* showed typical 9II + 9I association in 54% of the cells analyzed giving an average of 0.56 IV + 8.03 II + 9. 52 I per cell (Figs. 10-11). All the terads showed one to many micronuclei.

Pollen stainability and seed set - Pollen stainability in amphidiploids *E. coracana* and *E. africana* was about 98% and seed set was 95%, while in diploid *E. indica* and *E. tristachya* both the parameters were recorded as 97%. In *E. intermedia* and *E. floccifolia* the pollen stainability was 84% and 72%, while the seed set was estimated as 68% and 72% respectively. Triploid hybrids, though showed normal growth and substantial flowering, but the anthers were mostly shriveled with little content in them resulting in drastic reduction of pollen stainability which ranged between a meager 2-8% in F_1 hybrids. All these plants were completely seed sterile.



Figs. 1-11 — Male meiosis in diploid and tetraploid species of *Eleusine* and their F_1 hybrids. (1) Diakinesis showing 9II in *E. tristachya*. (2) Diakinesis showing 9II in *E. floccifolia*. (3) Diakinesis showing 18II in *E. africana*. (4) Diakinesis showing 1IV+8II+7I in *E. intermedia* x *E. coracana* F_1 hybrid. (5) Diakinesis showing 2IV+7II+5I in *E. intermedia* x *E. coracana* F_1 hybrid. (6) Diakinesis showing 9II+9I in *E. africana* x *E. indica* F_1 hybrid. (7) Diakinesis showing 10II+7I in *E. africana* x *E. indica* F_1 hybrid. (8) Diakinesis showing 9II+9I in *E. africana* x *E. floccifolia* F_1 hybrid. (9) Diakinesis showing 2IV+6II+7I in *E. africana* x *E. floccifolia* F_1 hybrid.(10) Diakinesis showing 10II+7I in *E. intermeida* x *E. africana* F_1 hybrid. (11) Diakinesis showing 1IV+7II+9I in *E. intermeida* x *E. africana* F_1 hybrid. (Small arrow showing Quadrivalents; Small arrowhead showing Univalents). Bar 10 μm.

DISCUSSION

To ascertain the number and type of genomes present in polyploids and detection of possible diploid progenitor species that led to the evolution of polyplid taxa is an important strategy of genome analysis in plants. Traditionally the genome analysis in polyploids has been achieved through study of chromosome pairing behaviour (KIHARA 1930) at prophase I of meiosis, considering the formation of bivalents as a direct reflection of homology between two genomes in question and lack of synapsis indicating no genetic affinity. Such studies carried out in several crop plants has provided authentic information on their origin and evolution on one hand (SIMMONDS 1976; GOTTSCHALK 1985, 1987; CHENNAVEERAIAH and HIREMATH 1991) and the phylogenetic interrelationships among various species on other hand. Although several limitations of genome analysis through this method has been emphasized by various workers (GAUL 1959; BENNETT 1984; GRANT 1987; JAUHAR and CRANE 1989). However chromosome pairing behavior has been clearly proved as a reliable method of genome analysis, next only to more empathetic approach of Genomic *In situ.* Hybridization (GISH) techniques (KIMBER *et al*. 1981; JAUHAR and CRANE 1989; RAINA and RANI 2001). Transfer of genes from wild to cultivated taxa to develop potential transgenics is gaining prominence now- a- days where such methods of genome analysis have a prominent role to play (GOODMAN *et al*. 1987).

The perusal of published literature confirms that *E. coracana* has a direct lineage from wild grass *E. africana* through selection followed by domestication (CHENNAVERRAIAH and HIREMATH 1974a). Both *E. coracana* and *E. africana* are amphidiploids with AABB genomes. To determine the true contributory species of A and B genome to *E. africana* and *E. coracana*, interspecific crosses involving these amphidiploids and suspected donor diploid species namely *E. intermedia*, *E. tristachya*, *E. indica*, and *E. floccifolia* have been attempted. The F_1 hybrids from all the cross combinations were characterized by the regular presence expected chromosome association of 9II + 9I, there by suggesting that all the four species might have contributed genomes in one way or other in the evolution of *E. africana* which has further given rise to *E. coracana*.

Earlier reports based on cellular and molecular genetic investigations on the amphidiploid *E. coracana* confirmed that *E. indica* is the A genome donor species (HILU 1988; HIREMATH and SALIMATH 1992; BISHT and MUKAI 2001, 2002).

The F_1 hybrid of *E. intermedia* x *E. coracana* had 78% of PMCs with 9II + 9I configuration. This pairing behaviour suggested that one of the genomes of *E. coracana* is homologous with the diploid *E. intermedia* genome. Does *E. intermedia* represents B genome donor or is it a primitive member of A genome group of species? Answer to this question lies in already established genomic relationship between *E. intermedia* and *E. indica* (unpublished data) which showed that 94% of PMCs in F_1 hybrid from this interspecific cross showed nine bivalents. Such pairing behavior suggest that *E. intermedia* genome has homology with *E. indica* and therefore it may be an AA genome species. Further morphologically *E. intermedia* and *E. indica* are quite similar and are often mistaken for each other. However, the former species can be separated from *E. indica* on the basis of three nerved as opposed to single nerved lemma in *E. indica* (PHILLIPS 1972). Karyotypes of *E. intermedia* and *E. indica* are also reported to be similar (SALIMATH 1990) confirming the close relationship of these two species. Thus *E. intermedia* is a primitive member of A genome group of species and is not a direct donor of A genome to the finger millet. It probably contains undifferentiated primitive AA genome from which *E. indica* (AA) genomes might have evolved. Thus, genomic symbol $A_{im}A_{im}$ is assigned to this species.

In F_1 hybrid of *E. tristachya* x *E. coracana,* 71% PMCs showed typical 9II + 9I associations implying that genome of *E. tristachya* belongs to A or B genomic group of *Eleusine*. This question may be resolved by analyzing the earlier published data of SALIMATH *et al*. (1995) who have observed complete homology between *E. tristachya* and *E. indica* (AA) through the chromosome pairing analysis of F_1 hybrid arising from the interspecific cross. Therefore it is suggested that *E. tristachya* belongs to A genomic group of *Eleusine*. Further *E. tristachya* is a distinct annual species with restricted distribution in south America and it nowhere grows sympatrically with *E. coracana*. Thus this species cannot be a direct A genome donor to *E. coracana* but belongs to A genome group of diploid Eleusines. Genomic symbol A_tA_t is assigned to this species. Our observations derive further support from molecular analysis of rDNA (HILU and JHONSON 1992) and genomic *in situ* hybridization analysis *E. coracana* (BISHT and MUKAI 2001)

About 74% of the PMCs of *E. africana* x *E. indica* hybrids had revealed the presence of 9II + 9I

which indicates that *E. indica* genome is homologous with one of the genomes of *E. africana* (AABB). Further, *E. indica* is morphologically similar to *E. africana* and often separation of these two taxa is difficult. *E. africana* is more robust, with wider spikes, longer lemma and palea than *E. indica*. The lower glume is one nerved in *E. indica* but it is three nerved in *E. africana*. From morphological basis and chromosome pairing data it is proposed that *E. indica* is one of the diploid progenitor of *E. africana* and genomic notation of A is assigned to *E. indica* (AA). Our observations derive complete support from earlier reports of (HILU 1988; HILU and JOHNSON 1992; HIREMATH and SALIMATH 1992; BISHT and MUKAI 2001) who have confirmed that *E. indica* is the A genome donor of *E. coracana* which is a direct descendent from *E. africana*.

In *E. africana* x *E. floccifolia* cross, the triploid hybrids had 9II+9I association in about 72.2% of the PMCs analyzed suggesting that one of the genomes of *E. africana* is homologous to the diploid *E. floccifolia*. Further, *E. floccifolia* is morphologically quite different from *E. coracana* and occupies different ecological niche. Therefore it is unlikely that *E. floccifolia* might have directly contributed A genome in the evolution of *E. africana*. It is in this context the observations of BISHT and MUKAI (2001; 2002) assume greater significance who have conclusively reported after performing double GISH experiments in *E. coracana* that the B genome has been contributed by *E. floccifolia* or an extinct relative of this species.

In *E. intermedia* x *E. africana* cross, the F_1 hybrids showed 9II + 9I association in 54% PMCs analyzed. Such chromosome pairing behaviour indicates that one of the genomes of *E. africana* is partially homologous with diploid *E. intermedia*. Earlier DEVARUMATH (1997) and SALIMATH (1990) through their cyto-morphological investigations on F_1 hybrids of *E. intermedia* x *E.indica* have also concluded that *E. intermedia* belongs to A genomic group of diploid *Eleusine* species.

From the foregoing discussion it is amply clear that *E. indica* with AA genome is pivotal donor species in the evolution of *E. coracana* and *E. africana* while *E. intermedia* ($A_{im}A_{im}$) and *E. tristachya* (A_tA_t) belong to A genomic group of diploid Eleusines. Further these three species form a close genetic assemblage within the genus *Eleusine*. The assumption that *E.floccifolia* is a definite B genome donor species is now widely accepted while *E. tristachya* might also be a candidate for BB genome is completely ruled out there by leaving the question wide open regarding identity of the other B genome donor species, if any.

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