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Quantitative nuclear DNA changes in *Eleusine* (*Gramineae*)

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Abstract: 2 C nuclear DNA amounts were determined in 30 collections belonging to 10 species of *Eleusine*. About a 2.5-fold variation in genome size is evident in the genus. The 2 C DNA amount in the diploid species ranged from 2.50 pg in *E. verticillata* to 3.35 pg in *E. intermedia*. In contrast, the tetraploid species showed a range from 4.95 pg in *E. africana* to 6.13 pg in *E. floccifolia*. At intraspecific level 10 collections of *E. coracana*, 6 of *E. indica*, 4 of *E. africana*, 2 of *E. tristachya*, and 2 of *E. kigeziensis* did not show any significant variation. However, 2 collections of *E. floccifolia*, connected with polyploidy, displayed about 90% variation. Polyploid species showed approximately double the genome size of that of their corresponding diploids. An evolutionary increase in DNA amount is evident in *E. coracana* during the course of its origin and domestication from *E. africana*.

Evolutionary divergence and speciation in higher plants has been accompanied by massive quantitative changes in 1 C nuclear DNA amount, ranging from 0.05 pg in *Cardamine amara* to 127.4 pg in *Fritillaria assyriaca*, an over 2500-fold variation (BENNETT 1985). DNA variation is evident at different phyletic levels. For example, within the *Leguminosae* there is a 36-fold DNA variation and it is still over 10 fold within some genera, e.g. *Crepis* (JONES & BROWN 1976, RAINA 1990). Even at the intraspecific level DNA variation is sometimes well pronounced (BENNETT 1985; OHRI & KHOSHOO 1986; PRICE 1976, 1988 a, b; MOWFORTH & GRIME 1989; RAINA 1990). Several mechanisms, such as lengthwise proliferation or deletion of segments, stochastic events, saltatory amplification, unequal crossing over, transposition and errors in DNA replication, have been cited as contributing to the nuclear DNA changes. Changes in genome size accompanying speciation do not follow any set pattern and evolutionary increase and decrease in DNA content are both common in plant species (PRICE 1988 a, b). In the present investigation a study has been made of the evolutionary pattern of change in genome size within the genus *Eleusine* GAERTN.

Eleusine (tribe *Eragrosteae*, family *Gramineae*), comprising 10–11 species, is predominantly distributed in Africa (PHILLIPS 1972). The 4 annual and 3 perennial

diploid species possess basic chromosome numbers of 8, 9, and 10. *E. africana*, *E. coracana* (both annual with 2n = 4x = 36), and *E. kigeziensis* (a perennial with 2n = 4x = 38) are allotetraploids (HIREMATH & CHENNAVEERAIAH 1982, SALIMATH 1990). *E. coracana*, commonly known as finger millet or ragi, is a cereal widely cultivated in East Africa and the Indian subcontinent. The cytogenetic mechanisms underlying speciation and evolution in the genus have been based hitherto on studies of karyotype, meiotic behaviour and interspecific hybridization (CHENNAVEERAIAH & HIREMATH 1991). In a genus where species differentiation accompanies only narrow changes in the chromosome complements, studies on the quantitative and qualitative changes in the nuclear genome would provide significant information about species relationships. In this context, the present investigation was designed to assess the extent of changes in genome size, both at intra- and interspecific level, accompanying the domestication of the *Eleusine* crop plants, vis-à-vis their wild progenitors. This communication deals with nuclear DNA amounts in 10 species of *Eleusine*, including 10 different collections of *E. coracana*, 4 of *E. africana*, 6 of *E. indica* and 2 in each of *E. tristachya*, *E. floccifolia*, and *E. kigeziensis*. An attempt has also been made to elucidate the phylogenetic and evolutionary trend within the genus following quantitative DNA changes.

Material and methods

The seed material was obtained from various germplasm banks, individual botanists and research organizations. Voucher specimens are deposited in the herbarium, Department of Botany, Karnatak University, Dharwad, India. Somatic chromosome numbers were determined in all the accessions and species by routine cytological methods (SALIMATH 1990). For DNA estimation, seeds of *Eleusine* species and *Allium cepa* were germinated on moist filter paper in petriplates. Actively growing root apices were excised and fixed in 1 : 3 acetic alcohol for 2 h. Then they were washed thoroughly in distilled water, hydrolysed in 5 N HCl for 30 min at room temperature and stained in leucobasic fuchsin (pH 2.2) for 2 h in total darkness. The stained root tips were given 3 washes of 10 min each in SO_2 water followed by a brief rinsing in distilled water. Finally, the stained root tips were squashed in a drop of glycerol on a glass slide. Three replicates of each material were prepared. Measurements of 2 C DNA amounts were made, using a Vickers M 86 Scanning Microdensitometer at 565 nm wavelength, of at least 15 telophase nuclei per replicate. The 2 C readings in arbitrary units were converted to pg, using the mean of a similar number of readings obtained for *Allium cepa* (2 C DNA = 33.5 pg, VAN'T HOF 1965), which was used as an internal standard. Readings were also taken of about five 4 C nuclei to cross-check the obtained 2 C values. The mean 2 C DNA value and standard deviation were calculated from the pooled data of replicates (Table 1), i.e. from three *Eleusine* slides.

Results and discussion

The species investigated, their habit, place of collection, 2 n chromosome number, and 2 C DNA amounts are given in Table 1. The genus *Eleusine* includes both diploid and polyploid species based on 3 basic chromosome numbers (HIREMATH & CHENNAVEERAIAH 1982, SALIMATH 1990). Among the diploid taxa *E. floccifolia*, *E. intermedia*, *E. tristachya*, *E. indica* and *E. verticillata* have 2n = 18 chromosomes, whereas *E. multiflora* and *E. jaegeri* have 2n = 16 and 20 chromosomes respectively. The tetraploid species *E. coracana* and *E. africana* have 2n = 4x = 36 and *E. kigeziensis* has 2n = 4x = 38 chromosomes.

Table 1. 2 C Nuclear DNA amounts in *Eleusine* species

Sample No.	Species	Place of collection	Life form	2n chrom. No.	2C DNA content (pg ± S.D.)
1.	*E. coracana* (L.) GAERTN.	Karnataka, India	Annual	36	5.64 ± 0.14
2.	*E. coracana*	Tamil Nadu, India	Annual	36	5.74 ± 0.14
3.	*E. coracana*	Uttar Pradesh, India	Annual	36	5.13 ± 0.18
4.	*E. coracana*	Rajasthan, India	Annual	36	5.77 ± 0.15
5.	*E. coracana*	Nepal	Annual	36	5.43 ± 0.18
6.	*E. coracana*	Uganda	Annual	36	5.34 ± 0.14
7.	*E. coracana*	Kenya	Annual	36	5.78 ± 0.17
8.	*E. coracana*	Malawi	Annual	36	5.52 ± 0.18
9.	*E. coracana*	Burundi	Annual	36	5.38 ± 0.11
10.	*E. coracana*	Ethiopia	Annual	36	5.46 ± 0.16
11.	*E. africana* KENNEDY O'BYRNE	Hattaragi, India	Annual	36	5.11 ± 0.18
12.	*E. africana*	Malawi	Annual	36	4.95 ± 0.14
13.	*E. africana*	Kenya	Annual	36	5.11 ± 0.14
14.	*E. africana*	Tanzania	Annual	36	5.11 ± 0.17
15.	*E. indica* (L.) GAERTN.	Howrah, India	Annual	18	2.93 ± 0.13
16.	*E. indica*	United States	Annual	18	2.73 ± 0.14
17.	*E. indica*	China	Annual	18	2.95 ± 0.15
18.	*E. indica*	Belgium	Annual	18	2.77 ± 0.14
19.	*E. indica*	Japan	Annual	18	2.89 ± 0.15
20.	*E. indica*	Tanzania	Annual	18	2.86 ± 0.11
21.	*E. tristachya* (LAM.) LAM.	Brazil	Annual	18	2.90 ± 0.12
22.	*E. tristachya*	Brazil	Annual	18	2.80 ± 0.11
23.	*E. verticillata* ROXB.	Aurangabad, India	Annual	18	2.50 ± 0.16
24.	*E. multiflora* HOCHST. ex A. RICH.	Kenya	Annual	16	2.60 ± 0.11
25.	*E. intermedia* (CHIOV.) S. M. PHILLIPS	Ethiopia	Perennial	18	3.35 ± 0.12
26.	*E. jaegeri* PILGER	Tanzania	Perennial	20	3.33 ± 0.17
27.	*E. floccifolia* (FORSSK.) SPRENG	Ethiopia	Perennial	18	3.26 ± 0.13
28.	*E. floccifolia*	Ethiopia	Perennial	36	6.13 ± 0.14
29.	*E. kigeziensis* S. M. PHILLIPS	Zaire	Perennial	38	5.93 ± 0.14
30.	*E. kigeziensis*	Burundi	Perennial	38	5.92 ± 0.14

In the present investigation 2 C nuclear DNA amount was estimated in 10 species of *Eleusine* involving 30 collections. A diagrammatic representation of the nuclear DNA variation with chromosome number and plant habit is depicted in Fig. 1.

Intraspecific variation. Among 10 species of *Eleusine, E. floccifolia,* exhibited intraspecific variation in 2C DNA amount (Table 1).

E. floccifolia (2n = 2x = 18, 2n = 4x = 36). *E. floccifolia,* the primitive taxon among Eleusines is generally a diploid species (2n = 2x = 18) with a symmetrical karyotype (HIREMATH & CHENNAVEERAIAH 1982). However, a race collected from Ethiopia has been shown to be autotetraploid (2n = 4x = 36) in origin (HIREMATH 1973, SALIMATH 1990). The 2C nuclear DNA values in the diploid and tetraploid cytotypes of *E. floccifolia* were observed to be 3.26 and 6.13 pg, respectively, showing an approximately two-fold variation. Such a variation is consistent with the nu-

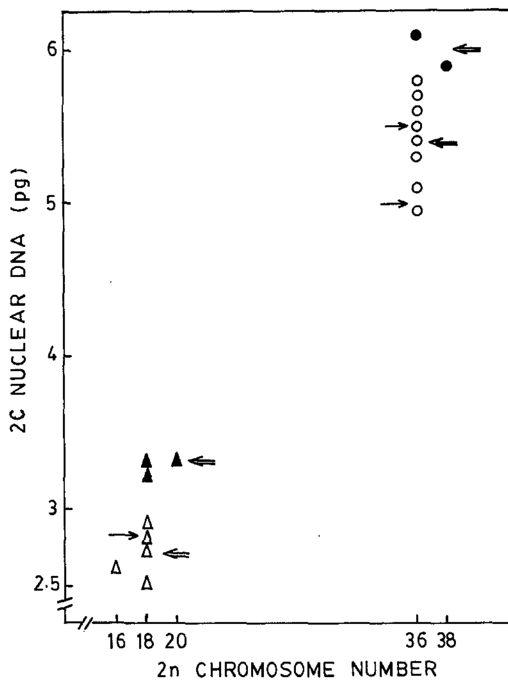

Fig. 1. 2 C nuclear DNA amounts in *Eleusine* spp. plotted against their somatic chromosome numbers. △ diploid annual, ▲ diploid perennial, ○ tetraploid annual and ● tetraploid perennial species. → mean of the accessions of a species, ⇐ group means of diploid annual and perennial; tetraploid annual and perennial species

merical change in the chromosome complement. A similar pattern of variation is reported in diploid and colchitetraploid cytotypes of some *Tephrosia* species (RAINA & al. 1986) and several such examples have also been reviewed by OHRI & KHOSHOO (1986). However, a minor change of 0.39 pg could well be interpreted as being due to the greater compaction or greater density of DNA in the tetraploid cytotype (VERMA & REES 1974).

E. indica (2n = 2x = 18). In the 6 collections of *E. indica* the 2 C DNA amount ranged from 2.73 to 2.95 pg with a mean value of 2.85 pg thus showing about an overall decrease of 8% from the highest to the lowest values. However, analysis of variance did not show significant differences between the accessions. *E. indica* is a highly polymorphic weed throughout the tropics and subtropics of the world, occupying the most diverse ecological habitats (PHILLIPS 1972). Cytogenetically it is an advanced species showing varying degrees of karyotype asymmetry (HIREMATH & CHENNAVEERAIAH 1982). On morphological and cytogenetical grounds it has been shown that *E. indica* and the diploid *E. floccifolia* have originated from a common ancestral genetic stock of *Eleusine* (SALIMATH 1990). Therefore, as *E. indica* is an advanced species with less DNA than *E. floccifolia*, it appears that the evolution of *E. indica* involves a decrease in genome size which may be of adaptive significance.

E. coracana (2n = 4x = 36). This species is a widely cultivated cereal in East Africa and Indian subcontinent. Five collections from East Africa and 5 from the Indian subcontinent had 2 C DNA values ranging from 5.13 to 5.78 pg with a mean value of 5.52 pg. This represents about 12% difference between highest and lowest values. Furthermore, analysis of variance showed significant differences ($p \leqslant 0.01$) between accessions. However, using Duncan's multiple range test ($\alpha = 0.05$) only one group, with a least significant difference of 0.67, was recognized. The DNA

values tend to follow a continuous distribution. Also, there is no significant difference between African and Indian cultivars.

CHENNAVEERAIAH & HIREMATH (1974) showed that *E. coracana* originated as a result of continuous selection and further cultivation of a large grain mutant of *E. africana* in the Ethiopian highlands. Later, HILU & DE WET (1976) concluded that *E. coracana* was domesticated as early as 5000 BC in an area between western Uganda and the Ethiopian highlands from which it reached the West Coast of India around 3000 BC. The racial differentiation in the recognized races of *E. coracana*, viz. cv. 'elongata', 'plana', 'compacta', 'vulgaris' all derived from the common race cv. 'coracana', occurred in Africa before it reached the Indian subcontinent (DE WET & al. 1984). This is confirmed by our finding of similar ranges of DNA value in African and Indian races.

E. africana (2n = 4x = 36). *E. africana* is a native to Africa thought not to occur outside Africa (PHILLIPS 1972), although one collection from India confirmed to be *E. africana* (HIREMATH & SALIMATH, unpubl.; THOMAS A. COPE, Kew, pers. comm.), was included in the present DNA study. Three of the 4 collections of this allotetraploid species showed 2 C DNA amounts of 5.11 pg while the remaining one had 4.95 pg. *E. africana* is a weed in the cultivation of *E. coracana* in East Africa and free gene flow between these two taxa is common (MEHRA 1962). The artificial F_1 hybrid between these two species exhibited regular 18 bivalents in nearly 88% of the PMCs and was fully fertile (CHENNAVEERAIAH & HIREMATH 1974). Furthermore, the F_2 and F_3 segregants were highly fertile, suggesting that the genomes of *E. coracana* and *E. africana* are very similar and that the two taxa are genetically conspecific (CHENNAVEERAIAH & HIREMATH 1974, HIREMATH 1974). In this context it is likely that further collections of these two species should show DNA amounts similar to those found in the present study.

E. coracana and *E. africana* are genetically conspecific allotetraploid taxa with AABB genomes (CHENNAVEERAIAH & HIREMATH 1974). Recently, independent studies by HILU (1988) and SALIMATH (1989) have shown that the annual diploid pantropical weed *E. indica* is the "A" genome donor of *E. coracana*. *E. coracana* and *E. africana* are advanced species within the genus and both show varying degrees of karyotype asymmetry. The karyotypes of these two taxa are similar in chromosome size, absolute chromosome length, type, and number of SAT chromosomes and satellite size (HIREMATH & CHENNAVEERAIAH 1982), although *E. coracana* has higher mean genome size, with about 12% more DNA than *E. africana*.

E. kigeziensis (2n = 4x = 38). Two collections of this allotetraploid species did not show any significant variation in their 2 C values (5.93 and 5.92 pg respectively).

E. tristachya (2n = 2x = 18). In this species the 2 C DNA amounts were 2.80 and 2.90 pg, again without any remarkable variation.

Observations presented above reveal an intraspecific DNA variation of the order of about 90% in *E. floccifolia*, reflecting a 2–4x difference. However, none of the remaining species possessed significant intraspecific DNA variation. Intraspecific variation in genome size, a recently-found phenomenon has so far been reported in only 24 species of angiosperms (RAINA 1990). Cytological and nuclear parameters, such as chromosome number, C value, and proportion of eu/heterochromatin represents the basic character of the organization of a genome and are relatively invariant in a stable species (NARAYAN & al. 1989). Any important changes in these

characters would, therefore, imply that the species is still in the process of evolution and fixation.

Interspecific variation. Species of *Eleusine* displayed about a 2.5-fold variation in genome size (Table 1), ranging from 2.50 pg in the diploid *E. verticillata* to 6.13 pg in the tetraploid race of *E. floccifolia*. The observed DNA amounts in diploids and tetraploids in the genus are depicted in Fig. 1 against their habit and somatic chromosome number. The diploid species showed a range in 2 C DNA value from 2.50 pg in *E. verticillata* to 3.35 pg in *E. intermedia*, with a mean of 2.96 pg. In contrast, among the tetraploid species the 2 C DNA amount varied from 4.95 to 6.13 pg in *E. africana* and *E. floccifolia* respectively.

The mean DNA amount in the tetraploids (5.66 pg) is about double that of the diploids (2.96 pg). This was further supported by regression analysis. The mean DNA amounts of groups of species with the same chromosome number were regressed on to their somatic chromosome number. The regression line was positive, linear and significant ($p \leqslant 0.001$) and the regression coefficient of the line "r" was 0.99. Both diploid and tetraploid taxa within the genus are annual as well as perennial with varying chromosome numbers. In the diploid annuals the mean DNA value (2.81 pg) is lower than that of the diploid perennial species (3.31 pg). *E. multiflora*, a diploid taxon with $2n = 16$, has a DNA amount of 2.60 pg, while *E. verticillata* with $2n = 18$ shows a smaller genome size despite its increased chromosome number. Similarly, *E. jaegeri* with $2n = 20$ has a genome size (3.33 pg) similar to that of *E. intermedia* (3.35 pg) which has $2n = 18$. It is evident that changes in DNA amount in different species have been achieved independently of changes in chromosome number. Similar observations have been reported in *Vicia* (RAINA 1990) and *Nicotiana* (NARAYAN 1987). Also, from the present study it is clear that there is no correlation between basic chromosome number and genome size as in case of *Allium* (LABANI & ELKINGTON 1987).

Diploid species of *Eleusine* show a narrow range of genome size variation, from 2.50 pg in *E. verticillata* to 3.35 pg in *E. intermedia*. Among annual and perennial diploid species the genome size varies from 2.50 pg to 2.85 pg and 3.26 pg to 3.35 pg respectively, the two groups of species exhibiting disjunct variation in DNA amounts. Despite this fact the annual and perennial species cross with each other easily and have close genomic affinities. For example, in F_1 hybrids between annual *E. tristachya* × perennial *E. floccifolia* and annual *E. indica* × perennial *E. floccifolia* nearly 70% and 80% respectively of the PMCs show regular 9 bivalents at diakinesis and MI (CHENNAVEERAIAH & HIREMATH 1973, SALIMATH 1990). The mean DNA amount of annual and perennial diploids is 2.81 and 3.31 pg respectively. Thus, as annuals are generally taken to be more advanced than perennials, a small amount of DNA reduction is apparent during their evolution in *Eleusine*. This has a direct bearing upon the origin of their respective polyploid species. An evolutionary decrease in DNA content from perennials to annuals is now well established (BENNETT 1972, OHRI & KHOSHOO 1986). Close examination of DNA variation among diploid annual and perennial species of *Eleusine* shows that species differentiation within these two groups has occurred without any remarkable change in DNA amount. For example, the annual *E. tristachya* and *E. indica* both show a mean of 2.85 pg DNA and have similar karyotypes showing varying degrees of asymmetry. Further, the interspecific hybrids between them reveal regular 9 biv-

alents in approximately 90% of the PMCs at diakinesis/MI and are partially fertile. So also, the perennial *E. floccifolia* and *E. intermedia*, with 3.26 pg and 3.35 pg DNA amounts, respectively, are both primitive taxa with similar symmetrical karyotypes (SALIMATH 1990). Similar differentiation of species without any significant change in DNA amounts has been reported in genera such as *Hordeum* (BENNETT & SMITH 1971, RAO & SHARMA 1987), *Amaranthus* (OHRI & al. 1981), *Ficus* (OHRI & KHOSHOO 1987), and *Vigna* (PARIDA & al. 1990).

Polyploidy is a conspicuous feature of chromosomal evolution in angiosperms and a prime facilitator of rapid speciation. In the *Gramineae* nearly 80% of the taxa are polyploid (GREILHUBER & EHRENDORFER 1988). Among *Eleusine* species *E. coracana* (2n = 36), *E. africana* (2n = 36), and *E. kigeziensis* (2n = 38) are allotetraploids whereas *E. floccifolia* (2n = 36) is an autotetraploid. The mean DNA content of *E. coracana, E. africana*, and *E. kigeziensis* is 5.52, 5.07, and 5.93 pg respectively, and in *E. floccifolia* it is 6.13 pg. Based on morphological and cytogenetical grounds it has been proposed that the diploid *E. jaegeri* (n = x = 10) and *E. indica* (n = x = 9) are the progenitors of *E. kigeziensis* (2n = 4x = 38) (SALIMATH 1990). The sum of the 2C DNA contents of *E. jaegeri* (3.33 pg) and *E. indica* (2.85 pg) is very close to the estimated 2C DNA value of *E. kigeziensis* (5.93 pg). Thus, in *Eleusine* there is a ploidy dependent DNA variation as has been reported in species of *Hordeum, Avena*, and *Larrea* (BENNETT & SMITH 1971, BULLEN & REES 1972, POGGIO & al. 1989).

CHENNAVEERAIAH & HIREMATH (1974) showed that *E. coracana* originated through selection and further cultivation of a "large grain mutant" of *E. africana*. The mean DNA content of *E. coracana* is 5.52 pg and that of its wild progenitor *E. africana* is 5.07 pg of DNA. It is apparent that there was a 10% evolutionary increase of DNA amount during the course of origin, evolution and domestication of *E. coracana* from *E. africana*. Domestication is an artificial selection under human observation, and little is known about the fate of DNA amount during its course in crop plants, with only limited numbers of studies available on this aspect. For example, Rice (*Oryza sativa*, originating from *O. perennis*) and Soybean (*Glycine max*, originating from *G. soja*) show significant reduction in their DNA amounts following domestication (NAGATO & al. 1981, YAMAMOTO & NAGATO 1984) whereas an oil seed crop niger (*Guizotia abyssinica*, originating from *G. scarba* subsp. *schimperi*) shows a marked increase in DNA amount (MURTHY 1987). However, in peanut (*Arachis hypogaea*) there is no marked change in DNA amount between it and its progenitor *A. monticola* (RESSLAR & al. 1981). The precise evolutionary significance of such variations remains to be elucidated.

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