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Trisomics in Pearl millet, *Pennisetum glaucum* (L.) R.Br.: Development and morphological variation

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Crosses between autotetraploid and diploid lines of *Pennisetum glaucum* (L.) R.Br. resulted in triploids. Progeny were obtained by selfing of F_1 triploids and/or backcrossing with diploid parent. Trisomic progeny were classified into seven groups based on their morphological characters. Seed-set was poor on trisomics (10–15 %). Transmission rates of the disomic (x + 1) gametes of different trisomics were high, ranging from 16.7 %–60.7 % although seed germination was poor (6.8 %). The progeny of each trisomic exhibited considerable morphological variation due to the heterogeneity resulting from differences in the genetic background of the parental accessions used unlike the uniformity found in earlier studies, where the autotetraploid parents were derived from the corresponding diploid parents.

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Pennisetum glaucum (L.) R.Br., a predominantly out-breeding species, is a cereal and fodder crop of considerable importance. It has shorter growing season requirements, tolerates higher temperatures and can be cultivated successfully in environments too hot and dry for Sorghum. In spite of its importance as a cereal crop in tropical and sub-tropical areas, little work has been done on its genetics when compared with that of wheat, rice, maize, sorghum, barley, tomato, potato, *Brassica*, etc. RAU (1929) determined the chromosome number of pearl millet as 2n = 2x = 14, while RANGASWAMY (1935) found seven bivalents with two terminalised chiasmata per pair at diakinesis. Since the initial discovery of trisomics in *Datura* (BLAKESLEE 1922), trisomic sets have been produced in several diploid species. Trisomic analysis has contributed considerably in establishing genetic linkage groups and assigning genes to chromosomes in Tomato (RICK and BARTON 1954), barley (TSUCHIYA 1958, 1959, 1960; SUBRAHMANYAM and AZAD 1978) and rice (KHUSH et al. 1984; MISHRA et al. 1985). Although trisomics have been produced in pearl millet (GILL et al. 1970; MANGA 1976; SAI KUMAR et al. 1982), the genetic back-grounds used to develop those trisomic sets were different (see ANAND KUMAR and ANDREWS 1993). MINOCHA and SIDHU (1979) determined the chromosomal location of 10 genes, using primary trisomics. Of these h_1 *(hairy leaf)* and Pg_1 *(purple glume)* are on chromosome 1; *Br (bristled earhead)*, *yst (yellow foliage striping)* and Pp_1 *(purple pigmented foliage)* are on chromosome 2; Pp_2 *(purple pigmented foliage)* is on chromosome 4; *Beb (branched earbase)* and Pn_1 *(purple node)* are on chromosome 5; and *Bet (branched eartip)* and Pg_2 *(purple glumes)* are on chromosome 6.

Merging of morphological marker-based and molecular marker-based maps of pearl millet is necessary to exploit complementarity of these tools in applied breeding programmes, which requires aneuploid stocks that were no longer available. The present paper describes the production of pearl millet trisomics from progeny of interploidy crosses, transmission rates, fertility, and morphological variations among their progenies.

Materials and methods

Seeds of autotetraploid and diploid lines of *Pennisetum glaucum* (x = 7), were obtained from Dr. Mengesha and Dr. Appa Rao, Genetic Resources Division, ICRISAT, Patancheru-502 324, India. The salient features of the lines used are presented in Table 1.

The land was ploughed and divided into plots. Seeds were sown manually at a spacing of 30 cm between plants in rows 30 cm apart. Irrigation was

Table 1. Morphological characters of *Pennisetum glaucum* (L.) R.Br. lines used

Accession* (x = 7)	Stock description	Other traits
IP 12433 (4x)	Thick and dark green leaves with a thick and compact panicle	Glabrous leaves, green nodes
IP 12434 (4x)	Thick and dark green leaves with a thick and compact panicle	Glabrous leaves, purple nodes
IP 12435 (4x)	Thick and dark green leaves with a thick and compact panicle	Glabrous and erect leaves, purple nodes
IP 5009 (2x)	Normal green foliage/nodes	Glabrous leaves
IP 8166 (2x)	Whole plant purple with green nodes	Hairy stem, glabrous leaves, ring of purple hairs around nodes

* Source: Genetic Resources Division, ICRISAT Centre Patancheru - 502 324, India

provided whenever necessary, and hand weeding was done. 0.5 % Dimethoate (Rogor) was sprayed once in a month to check insect damage and 0.25 % carbendazim (Bavestin) to prevent fungal diseases.

Reciprocal crosses were made between autotetraploid and diploid lines of *Pennisetum glaucum*, in which anthesis commences at sunrise and the anther dehiscence will be complete in about 2 h. Anthesis of different florets may be spread over a three-day period. *P. glaucum* being protogynous (BURTON and POWELL 1968), the panicles, as they began to emerge from the boot, were covered with glassine bags to prevent stray pollination. Pollen parents were bagged in the evenings and the pollen was collected for crossing on the following morning. Pollen collected from a single plant was dusted on to stigmas of the female parent. Since the florets start maturing from top to bottom, each panicle was pollinated on three consecutive days, by which time all the stigmas would wither. After confirming that all the stigmas had withered the glassine bags were removed from the panicles and the crossed panicle was labelled.

To determine the chromosome number of parental and progeny plants, root-tips were collected during the fore-noon in prechilled distilled water and kept at 4°C overnight followed by fixing in 1 part of glacial acetic acid and 3 parts of ethanol for up to 24 h. They were later transferred to 70 % ethanol and stored until use. The root-tips were treated with 0.05 % pectinase at room temperature (30°C approx.) for 1 h, stained and squashed in 2 % acetocarmine. For meiotic studies, florets of appropriate sizes were collected 2 h after sunrise in Carnoy's fluid (6:3:1 ethanol, chloroform and glacial acetic acid). After 24 h they were transferred to 70 % ethanol and stored at 4°C until use. Anthers from the appropriate florets were squashed in 2 % acetocarmine. Observations were made on chromosomal configurations. Pollen stainability in 1 % acetocarmine was taken as an index of pollen fertility. All shrivelled and poorly stained grains were counted as sterile. Pollen fertility levels were recorded for the aneuploids and diploid lines. The triploids and aneutriploids obtained from the above crosses were selfed and/or backcrossed with diploid stocks, and chromosome numbers of the progeny were determined as described above. Aneuploids were maintained by selfing and/or crossing with the diploid line (IP 8166). The seeds were sown in trays, confirmed trisomics were transferred to larger pot(s) or transplanted in the field.

Based on the morphology, the trisomic progeny were identified in the F_2 generation. Data on plant height, tiller numbers, internode numbers, stem girth, panicle length and girth were collected as follows:

Plant height: Height of the plant was recorded at maturity. The measurements were taken from the ground level to the tip of the tallest panicle.

Tiller number: The panicle-bearing tillers were counted at maturity.

Number of internodes: Numbers of nodes of the tallest tillers were counted.

Stem girth: Stem girth was measured by encircling a tape around the middle portion of the third internode.

Spike length and girth: The length of the longest panicle and its girth were recorded.

Table 2. Results from crosses between autotetraploid and diploid lines of *Pennisetum glaucum* (L.) R.Br.

Parents (x = 7)		Number of			Progeny with chromosome number						
Seed	Pollen	Crosses	Seeds		14	18	20	21	22	23	24
			Obtained	Sown*							
IP 12433 (4x)	IP 5009 (2x)	21	151	76 (50.0)	11	–	–	1	–	–	–
	IP 8166 (2x)	3	46	45	–	–	1	18	–	1	–
IP 12433 (4x)	IP 5009 (2x)	31	62	26 (76.9)	1	–	–	2	–	–	–
	IP 8166 (2x)	15	20	14 (21.4)	–	–	–	3	–	–	–
IP 12435 (4x)	IP 5009 (2x)	11	131	123 (36.6)	2	–	–	3	1	–	–
	IP 8166 (2x)	8	67	28 (46.4)	–	1	–	3	–	–	1
IP 5009 (2x)	IP 12435 (4x)	3	16	16 (100)	16	–	–	–	–	–	–
	IP 12433 (4x)	8	26	26 (42.3)	11	–	–	–	–	–	–
IP 8166 (2x)	IP 12434 (4x)	13	38	38 (86.8)	33	–	–	–	–	–	–

* % germination given in parenthesis

Results

Autotetraploid lines pollinated with diploids of *Pennisetum glaucum* resulted predominantly in triploid progeny (Table 2). Progeny from the cross IP 12433 (4x) × IP 5009 (2x) (green) consisted of one triploid (3x) and eleven dihaploids (2x). The same tetraploid line pollinated with diploid line IP 8166 (purple) yielded eighteen triploids, one with 20 chromosomes and another with 23 chromosomes. Crosses between IP 12434 (4x) and IP 5009 (2x) gave two triploids (3x) and one dihaploid (2x), while the same tetraploid line pollinated with IP 8166 (purple) gave three triploids. IP 12435 (4x) crossed as seed parent with IP 5009 (2x), resulted in three triploids (3x), one tetrasomic triploid (with 22 chromosomes) and two dihaploids (2x). Crossing IP 12435 with IP 8166 (purple) pollen resulted in purple progeny which included three triploids, one hypotriploid (18 chromosomes), and one hypertriploid (24 chromosomes). Reciprocal crosses using pollen from tetraploids gave 14-chromosome plants, which were morphologically similar to their seed parents. The triploid plants produced 4–8

Table 3. Metaphase I chromosome configurations and pollen stainability in *Pennisetum glaucum* triploids and aneutriploids derived from autotetraploid × diploid crosses

Parentage	Chromosome number		Cells analysed	Metaphase I configurations*				Stainable pollen %
	Gametes	Zygote		I	II	III	IV	
IP 12435 × IP 8166	11 7	18	84	3.44	5.04 (1–4)	1.39 (1–7)	– (0–3)	8.0
IP 12433 × IP 8166	13 7	20	–	–	–	–	–	10.9
IP 12433 × IP 8166	14 7	21	103	2.72	2.71 (0–6)	4.25 (0–6)	– (1–7)	7.6
IP 12435 × IP 5009	15 7	22	–	–	–	–	–	16.7
IP 12435 × IP 8166	17 7	24	101	6.27	4.10 (2–9)	2.88 (3–6)	0.16 (2–7)	66.9 (0–2)

I-Univalents, II-Bivalents, III-Trivalents, IV-Quadrivalents
* Range in parenthesis

Table 4. Pedigree of the trisomic (2x + 1) plants produced

Pedigree (x = 7)	(2x + 1)	Group
IP 12433 (4x) × IP 5009 (2x)→3x (08) selfed	TS-08	I
IP 12433 (4x) × IP 5009 (2x)→3x (01) × IP 8166 (2x)	TS-09	
IP 12433 (4x) × IP 5009 (2x)→3x (02) × IP 8166 (2x)	TS-10	
IP 12434 (4x) × IP 5009 (2x)→3x (25) × IP 8166 (2x)	TS-24	
IP 12433 (4x) × IP 8166 (2x)→3x (30) selfed	TS-26	
IP 12433 (4x) × IP 8166 (2x)→3x (18) × IP 8166 (2x)	TS-30	
IP 12433 (4x) × IP 5009 (2x)→3x (01) × IP 8166 (2x)	TS-01	II
IP 12434 (4x) × IP 5009 (2x)→3x (25) × IP 8166 (2x)	TS-27	
IP 12433 (4x) × IP 8166 (2x)→3x (29) × IP 8166 (2x)	TS-07	
-do-	TS-18	
IP 12433 (4x) × IP 8166 (2x)→3x (27) × IP 8166 (2x)	TS-22	
IP 12433 (4x) × IP 5009 (2x)→3x (02) × IP 8166 (2x)	TS-05	III
IP 12433 (4x) × IP 8166 (2x)→3x (29) × IP 8166 (2x)	TS-11	
-do-	TS-13	
IP 12433 (4x) × IP 8166 (2x)→3x (27) × IP 8166 (2x)	TS-20	
IP 12433 (4x) × IP 5009 (2x)→3x (02) × IP 8166 (2x)	TS-03	IV
IP 12433 (4x) × IP 8166 (2x)→3x (29) × IP 8166 (2x)	TS-29	
IP 12433 (4x) × IP 5009 (2x)→3x (02) × IP 8166 (2x)	TS-02	V
-do-	TS-04	
IP 12433 (4x) × IP 8166 (2x)→3x (26) × IP 8166 (2x)	TS-06	
-do-	TS-21	
IP 12433 (4x) × IP 8166 (2x)→3x (29) × IP 8166 (2x)	TS-14	
IP 12433 (4x) × IP 5009 (2x)→3x (02) × IP 8166 (2x)	TS-15	VI
-do-	TS-16	
-do-	TS-23	
IP 12433 (4x) × IP 8166 (2x)→3x (27) selfed	TS-28	
IP 12433 (4x) × IP 8166 (2x)→3x (29) × IP 8166 (2x)	TS-12	VII
-do-	TS-17	
IP 12435 (4x) × IP 5009 (2x)→3x (21) × IP 8166 (2x)	TS-25	
IP 12435 (4x) × IP 5009 (2x)→3x (14) × IP 8166 (2x)	TS-19	

tillers and had longer panicles than their diploid parents. The majority of the triploids produced nodal aerial branches but the seed-set was poor. Progeny with 18, 20, 22, 23, 24 chromosomes were indistinguishable morphologically from their corresponding triploid sibs.

Metaphase I configurations and pollen stainability among the progeny from interploidy crosses are presented in Table 3. The hypotriploid (2n = 18) showed a low frequency of trivalents (1.39/cell) with a maximum of three per cell and a high frequency of univalents (3.44/cell),with a maximum of four per cell. This represented over 56 % of the complement as bivalents and 23 % as trivalents. Only 8 % pollen was stainable. The disomic- (2n = 20) and tetrasomic- (2n = 22) triploids showed 10.9 % and 16.7 % stainable pollen, respectively (Table 3). In triploids (2n = 3x = 21) a high proportion (61 %) of the chromosomes formed trivalents, 26 % were bivalents, and 13 % were univalents. All possible anaphase I disjunctions were evident with occasional laggards. Only 7.6 %

Table 5. Phenotypic variation among the seven primary trisomic groups in *Pennisetum glaucum* (L.) R. Br.

Trisomic Group*	Height (mm)	Tiller number	Internode number	Stem girth (mm)	Panicle	
					length (mm)	girth (mm)
I	246 ± 25.5	1.4 ± 0.24	4.2 ± 0.55	9 ± 0.4	81 ± 3.2	31 ± 0.4
II	341 ± 21	4.5 ± 0.95	3.5 ± 0.29	10 ± 0.2	107 ± 7.8	35 ± 0.2
III	462 ± 13.4	2.8 ± 0.86	3.0 ± 0.32	10 ± 0.2	112 ± 3.7	36 ± 0.5
IV	596 ± 8.1	2.7 ± 0.23	2.7 ± 0.33	12 ± 0.3	143 ± 3.3	38 ± 0.3
V	692 ± 22	0.8 ± 0.00	4.6 ± 0.24	13 ± 0.3	111 ± 7.1	39 ± 0.2
VI	902 ± 42	1.5 ± 0.00	4.7 ± 0.43	16 ± 0.8	113 ± 5.6	39 ± 0.25
VII	1230 ± 4.1	2.3 ± 0.33	6.3 ± 0.33	21 ± 0.7	150 ± 3.0	51 ± 0.32

* Plants same as in Table 4

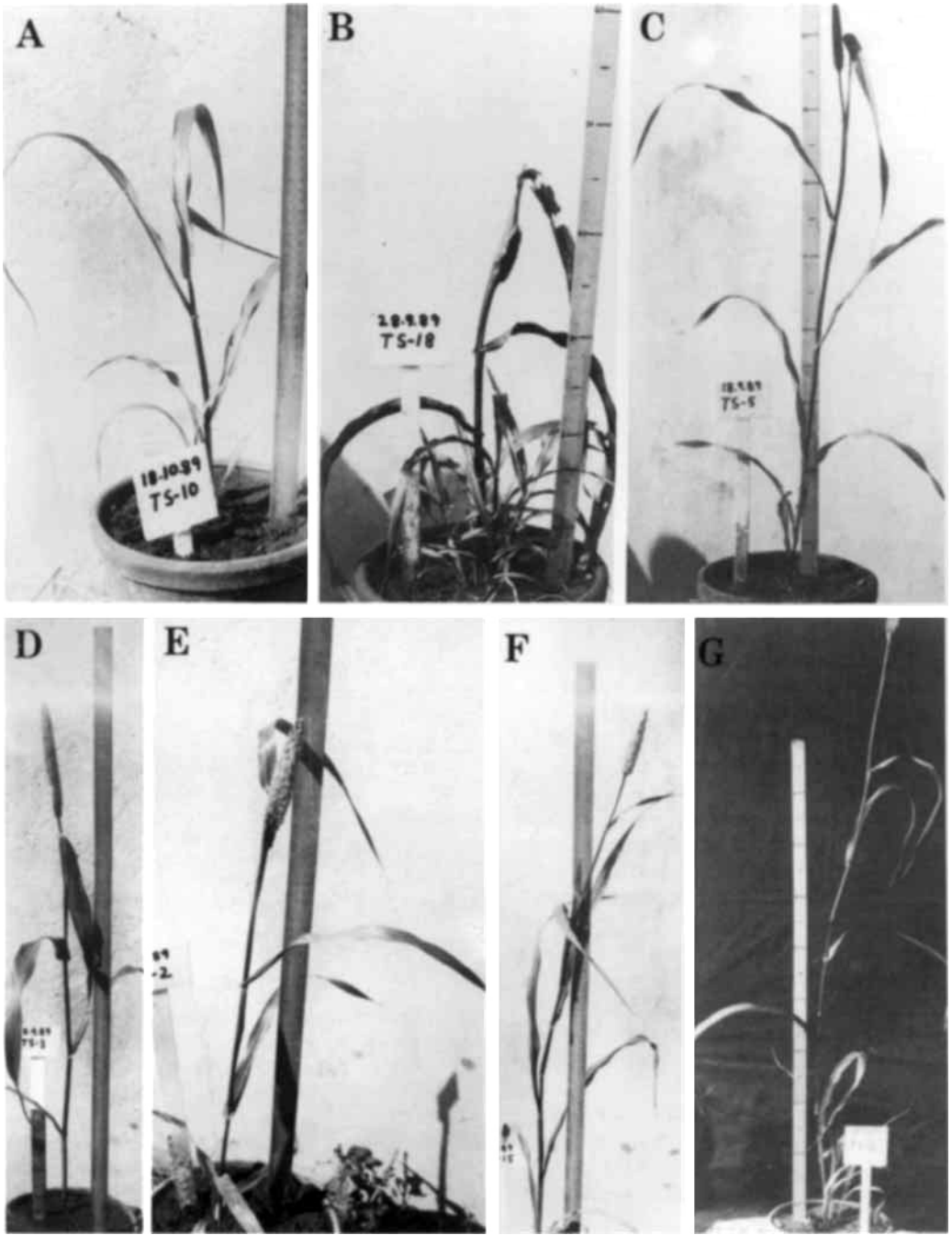

Fig. 1A–G. Representative from trisomics groups I to VII respectively: **A,** 44 days old (I); **B,** 64 days old (II); **C,** 64 days old (III); **D,** 74 days old (IV); **E,** 75 days old (V); **F,** 64 days old (VI); and **G,** 64 days old (VII). (Note differences in morphology and maturity.)

Table 6. Transmission frequency of extra chromosome among the groups of trisomics in *Pennisetum glaucum* (L.) R. Br.

Trisomic		Germination	Progeny with chromosome numbers				Trisomic % (*)
Group	Plant No.		14	15	16	21	
I	TS-08	0/20	–	–	–	–	
	TS-10	4/66	3	1	–	–	
	TS-26	15/148	10	4	–	1	
	TS-30	9/40	6	3	–	–	
	Total	28/274	19	8		1	28.6 (20.9)
II	TS-27	4/122	2	1	1	–	
	TS-22	17/70	16	1	–	–	
	TS-18	3/150	1	2	–	–	
	Total	24/342	19	4	1		16.7 (30.5)
III	TS-05	5/159	3	2	–	–	
	TS-20	3/145	1	2	–	–	
	TS-11	20/150	6	13	1	–	
	Total	28/454	10	17	1		60.7 (29.0)
IV	TS-03	8/10	8	–	–	–	
	TS-29	27/163	10	17	–	–	
	Total	35/173	18	17			48.6 (16.1)
V	TS-02	0/126	–	–	–	–	
	TS-06	14/300	6	8	–	–	
	Total	14/426	6	8			57.1 (19.5)
VI	TS-15	28/541	19	9	–	–	
	TS-28	9/125	5	4	–	–	
	Total	37/666	24	13			35.1 (20.5)
VII	TS-12	20/390	16	4	–	–	20.0 (15.2)

(*) Transmission % reported by MINOCHA and SIDHU (1981)

pollen was stainable (Table 3). The plant with 24 chromosomes showed 27 % univalents, 34 % bivalents, 37 % trivalents, and 3 % quadrivalents at metaphase I and a high proportion (66.9 %) of stainable pollen when compared with other aneutriploids (Table 3).

Triploids were pollinated with the purple diploid line IP 8166 and/or selfed. The progeny were screened for their chromosomal constitutions. Pedigrees of thirty trisomics ($2n = 2x + 1 = 15$) are presented in Table 4. These primary trisomics were distinguishable from their diploid sibs. Trisomics were generally weak, with small panicles and showed poor seed-set. These thirty trisomics were classified into seven groups (Table 5, Fig. 1) based on their morphological features as was done earlier by GILL et al. (1970).

Group I: Short with tiny panicle, one or two secondary tillers.

Group II: Dark green leaves, comparatively taller than group I plants with medium size panicle, profuse tillering on transfer to the field, and short internodes.

Group III: Narrow leaves, weak stem, and long internodes.

Group IV: Plants are slender with slender panicles.

Group V: Thick and spindle-shaped panicles.

Group VI: Plants are short, broad leaves, and late flowering.

Group VII: Resemble the diploid but for its weak stem, poor tillering and small leaves.

The trisomics ($2x + 1$) belonging to each group were selfed and/or backcrossed with diploid IP 8166 as pollen parent, and the results on the transmission frequencies of the $x + 1$ gametes among the groups of trisomics are presented in Table 6. The seed-set was invariably poor in all the trisomics. Self-pollinations of trisomics yielded very few or no seeds. Germination of seed from the trisomics was generally very low. In trisomic group I, 28 out of 274 seeds germinated. Eight of the progeny were trisomics, 19 were diploids, and one had 21 chromosomes, which could have resulted from fertilization with a 14 chromosome gamete

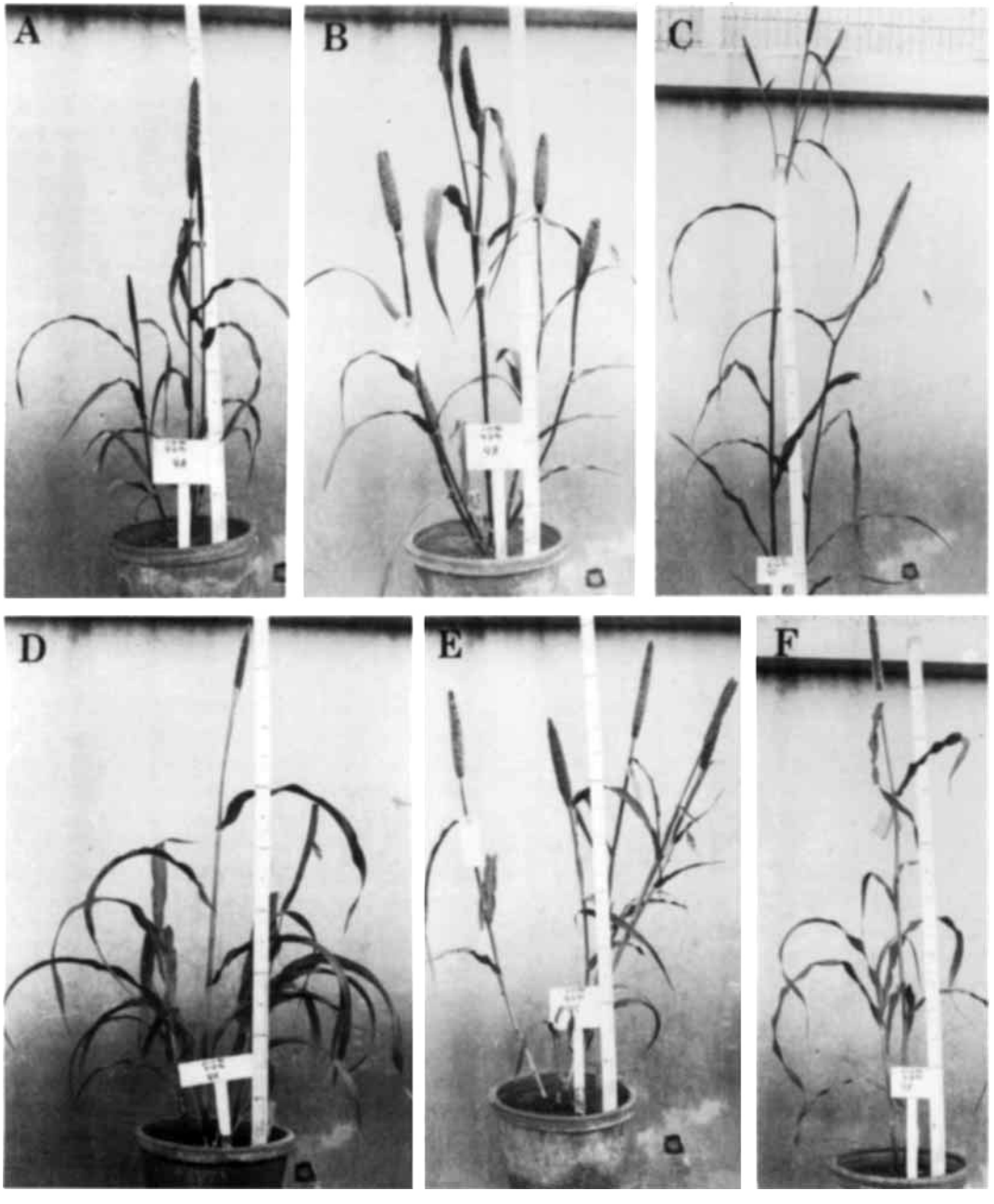

Fig. 2A–F. Trisomic progeny from a group IV trisomic: **A, B and C** 95 days old; **D and F** 75 days old and **E** 95 days old. (Note differences in tillering and its synchrony, height, branching and maturity.)

following restitution. Among group II trisomics, 24 out of 342 seeds germinated. Four were trisomics, one was a double trisomic, and 19 were diploids. From group III, 28 out of 454 seeds germinated. Seventeen were trisomics, one was a double trisomic, and 10 were diploids. Out of 173 seeds from trisomics of group IV, 35 germinated, of which 17 were trisomics and 18 were diploids. In group V, 14 out of 426 seeds germinated. Eight were trisomics and 6 were diploids. From trisomic group VI, 37 out of 666 seeds germinated, 13 were trisomics and 24 were diploids. Group VII trisomics had a trivalent associated with nucleolus. Among the 20 (out of 390) seeds germinated, 4 were trisomics and 16 were diploids. The morphological features of trisomic progeny within each group exhibited considerable variation. Trisomic progeny from a group IV trisomic is presented in Fig. 2.

Discussion

The autotriploids of *P. glaucum* (Table 2) were expected in the F_1 of crosses between autotetraploid (IP 12433, IP 12434, and IP 12435) and diploid (IP 5009 and IP 8166) lines. The aneutriploids with 18 and 24 chromosomes must have resulted from the fertilization of 11- and 17-chromosome gametes of the seed parent by the 7-chromosome male gamete. These 11- and 17-chromosome gametes could be the complementary meiotic products in autotetraploids ($2n = 4x = 28$). The high frequency of 14-chromosome (dihaploid) progeny from crosses involving autotetraploids as seed parent (Table 2) are likely to represent parthenogenetic development of dihaploid egg cell following pollinations. The exclusive production of 14-chromosome plants (which were similar to their respective diploid seed parent) in the reciprocal cross may indicate that the 2x pollen from the male parent may be ineffective due to their slower rate of germination and/or growth through the diploid stylar tissue, and that 1x pollen from some of the spikelets of the seed (diploid) parent may have been able to compete successfully. A possibility of apomixis in the diploid seed parent could not be ruled out in the absence of experimental data at present.

The morphological variations among the trisomics might be attributable to different extra chromosome in each of the trisomics. In all these trisomics, different levels of heterozygosity or homozygosity are to be expected since the genotypes of the tetraploid and diploid parents were different, and the parental lines themselves were not necessarily homozygous.

The transmission frequencies of the trisomic condition in pearl millet were previously reported to be poor (MANGA 1976; MINOCHA et al. 1976; SINGH et al. 1984). MINOCHA et al. (1976) observed that selfed progenies of the trisomics yielded 3.4 % trisomic progeny, and in the crosses trisomic × diploid and diploid × trisomic, trisomics constituted 7.7 and 1.3 % respectively, while MANGA (1976) recorded a maximum of 14 % for any chromosome either through selfing or crossing with diploid. Transmission rates of $x + 1$ gametes through the female ranges from 15.5 to 43.9 % in rice (KHUSH et al. 1984). Theoretically one expects a $2x + 1$ plant to produce x and $x + 1$ gametes in equal frequency, which should be reflected in the frequencies of the 2x and $2x + 1$ progeny. However, from the data so far available on trisomics of different plant species (HERMSEN 1970; KHUSH 1973; HO and KASHA 1975) such expectations are never realised, and the percentage of $2x + 1$ progeny of trisomics is much lower. In our study, fairly good transmission rate of the extra chromosome was observed for all the trisomics. This is attributable to the heterozygosity resulting from differences in the genotypes of the tetraploid and diploid parents used, as distinguished from the low frequencies of $2x + 1$ progeny of the trisomics derived from crosses between induced autotetraploid and diploid parents derived from single accessions (MINOCHA et al. 1976; MANGA 1976). The seed germination for all the seven trisomics of pearl millet in the present study was very poor.

Most of the trisomics showed considerably low pollen fertility. It is conceivable that the reduced vigour and fertility of trisomics result from genic imbalance(s) caused by the three doses of a specific chromosome compared with the two doses on the other chromosomes (MISRA et al. 1985).

Data on crosses of these trisomics with seven different morphological markers (NAGESH 1994) revealed trisomic segregation for genes d_3 *(dwarf)* and *tgr (tigrina leaf)* with triplo-1; Pp_1 *(purple plant), Beo (earhead bearing orange bristles)* and gl_1 *(glossy)* with triplo-2; *Fbb (florets bearing bristles)* with triplo-3; and *VLBr (very long bristles)* with triplo-5; while triplo-7 is a trisomic for the nucleolar organizer. Further studies with additional chromosome-specific markers (ANAND KUMAR and ANDREWS 1993; MINOCHA and SIDHU 1979)

are in progress to tag independent loci to distinguish triplo-4 from triplo-6. The present set of trisomics can now be used to assign chromosomes of the morphological marker-based map to linkage groups of the pearl millet molecular marker-based map (LIU et al. 1994). This would facilitate identification of additional chromosome-specific markers to develop a comprehensive chromosome-specific reference map of pearl millet for marker-assisted selection applications.

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