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Transmission of primary trisomics in pearl millet

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Summary. Transmission rates of extra chromosomes found in the full set of trisomics of pearl millet (*Pennisetum americanum*) ($2n = 14$) were estimated by examining the progeny of selfed trisomics and the progeny of trisomics crossed to disomics. When the trisomics were selfed, 'dark green' and 'tiny' had the highest transmission rate (23.8% and 23.3%, respectively) and 'pseudonormal' the lowest (13.8%). Other trisomics had an intermediate rate of transmission. When the trisomics were used as females in crosses with disomics, both 'dark green' and 'tiny' again had the highest transmission rate and 'pseudonormal' the lowest. When the trisomics were used as males in crosses to disomics, no trisomic was transmitted to the progeny except for 'spindle', and this occurred with a very low frequency (2.0%). A variation in transmission rate was observed from plant to plant and season to season for the same trisomic type. A study of the transmission rate of the extra chromosomes indicated that the following factors were probably contributing to the lower rate of transmission: small- or light-weight seeds tended to have a higher proportion of trisomics than heavier seeds; lighter seeds had a lower percentage germination; a positive and significant correlation was noticed between trivalent frequency and transmission rate. Plants with reduced vigour produced a higher frequency of trisomics. Though trisomics involving longer extra chromosomes showed a high degree of pollen and ovule sterility, they were highly transmissible. This has resulted in a close relationship between gametic sterility and transmission rate of extra chromosome.

Key words: Chromosome transmission – Pearl millet – Trisomic series – Trivalent frequency

Introduction

In many diploid species transmission rates of $n+1$ gametes in various trisomics are much less than the expected 50% (Chen and Grant 1968; Kamnoi and Jenkins 1962; Kasha and McLenan 1967; Palmer 1976; Schertz 1966; Virmani 1969). The reduced transmission rate of the extra chromosomes in trisomics is attributable to many factors (Khush 1973) but the relative importance of each factor can vary from species to species or from trisomic to trisomic. With a few exceptions, there is a significant difference between pollen and ovule transmission of the extra chromosomes; the transmission rate through the ovules tends to be much higher than through the pollen (Goodspeed and Avery 1939; Rick and Barton 1954). However, the degree of difference between pollen and ovule transmission not only varies from species to species but also fluctuates from chromosome to chromosome. In pearl millet the transmission rate through the ovules tends to be much higher than through the pollen (Virmani 1969). A study on transmission rate of trisomic is highly useful in understanding the degree of maintenance of trisomics and in locating genes on the extra chromosomes. Primary trisomics have been used in locating some markers to specific chromosomes of pearl millet (Minocha and Sidhu 1979). Certain factors, such as seed weight, germination percentage, trivalent frequency, plant size and pollen sterility, have been found to affect the transmission rate of the extra chromosomes in six trisomics of *Sorghum* (Liang 1979).

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The objective of this report is to examine the transmission rate of seven primary trisomics of pearl millet and the relative importance of factors that affect the transmission rate of the extra chromosomes.

Materials and methods

Transmission rates of seven primary trisomics (tiny, dark green, lax, slender, spindle, broad and pseudonormal) originated from triploid pearl millet were analysed. The transmission rates and germination percentages of these trisomics with respect to seed weight were determined only once in the main crop season of 1979. Seeds obtained from selfed trisomics and from trisomic × disomic crosses were divided into two groups, big and small, on the basis of their test weight. Germination percentages in both classes of seeds were recorded in every season of crop. Thus, the effect of the four factors germination percentage, plant size, trivalent frequency and gametic sterility on transmission rate was assessed in four different seasons of crops (one main and one off-season in each of the years, 1979 and 1980). Seeds of selfed trisomics, of open-pollinated trisomics and of disomic × trisomic crosses were germinated in pots and the complete series of trisomics thus obtained were maintained along with normal disomics (2n = 14). Plant size was determined on the basis of plant height of trisomics relative to that of disomics at the time of harvest. Trisomic plants were shorter than disomics plants. PMC's from each plant were collected and fixed in modified Carnoy's fluid for 24 h at room temperature and then stored in 70% alcohol under refrigeration (10 °C) until examined. Anthers were squashed in 2% aceto-carmine to determine the chromosome number and meiotic configurations of each trisome. Pollen and ovule sterility of different trisomics and the control H-8 were also examined.

Plant to plant variation in transmission rates was analysed in each of the four crop seasons and the relative importance and combined effects of the contributing factors to transmission rates of the extra chromosomes were also determined following standard partial regression and multiple correlations, respectively.

Results and discussion

Transmission rates of the extra chromosomes varied from chromosome to chromosome (Table 1). For selfed trisomics (seeds of all sizes from each panicle were included), the percentage of trisomic offspring was highest for dark green (23.8%) and lowest for pseudonormal (13.8%). The transmission rates for selfed trisomics could be divided into three categories; high for dark green and tiny; medium for spindle, broad, lax and slender; low for pseudonormal. When the trisomics were used as females in crossing with the disomics, or left open-pollinated, transmission rates of the extra chromosome through the ovule followed the same pattern as that of selfing. Dark green recorded the highest transmission rate of extra chromosomes and pseudonormal the lowest. When the trisomics were used as pollen parents in crossing with disomics, only spindle had a very low percentage of pollen transmission (2.0%), while other trisomics failed to transmit their extra chromosomes. This result agreed with those of Virmani (1969) who also noted a low pollen transmission in only two trisomics (dark green and spindle, with the frequencies of 3.7% and 1.0%, respectively) of pearl millet. Similarly, in case of pearl millet no tertiary trisomic has been found to be transmitted through pollen (Singh et al. 1982).

Transmission rates of the extra chromosomes varied from plant to plant for the same trisomic, and the two trisomics, tiny and dark green, showing a higher transmission rate, tended to vary the most. Variation in transmission rate from plant to plant for a few trisomics is shown in Table 2. These findings are in accordance with those of Liang (1979) who noted plant to plant variation in transmission rates of six trisomics of *Sorghum*. Transmission rates also varied from year to year for the same trisomics. Rajhathy (1975) noticed that growing conditions also exert some influence on the trisomic transmission in *Avena strigosa*. Plant to plant and season to season variation in trisomic transmission may be attributed to sampling variation. Causes for variation in transmission rate from plant to plant are undetermined. Because of plant to plant

Table 1. Transmission rates of the extra chromosomes for seven primary trisomics in pearl millet

Trisomic type	Self pollination			Trisomics × Disomics			Disomics × Trisomics		
	Plants examined no.	Trisomics		Plants examined no.	Trisomics		Plants examined no.	Trisomics	
		No.	%		No.	%		No.	%
Tiny	30	7	23.3	124	22	17.7	68	0	0
Dark green	84	20	23.8	76	14	18.4	56	0	0
Lax	74	12	16.2	136	20	14.7	84	0	0
Slender	146	22	15.1	836	120	14.4	320	0	0
Spindle	36	6	16.7	94	15	16.0	50	1	2.0
Broad	134	22	16.4	224	29	12.9	116	0	0
Pseudonormal	218	30	13.8	630	75	11.9	256	0	0
Total/average	722	119	16.5	2 120	295	13.9	950	1	0.1

Table 2. Variation in transmission rates of the extra chromosome among plants of two primary trisomics crossed with disomics in pearl millet

Tiny			Dark green		
Designation	No.	%	Designation	No.	%
GH-162[a]	2/4	50	3-1A-8-1[a]	3/6	50
TR-89[a]	3/5	60	358[a]	2/5	40
33[a]	2/6	33	TR-73[a]	6/10	60
TR-89	6/22	27	GH-13[a]	2/5	40
33	4/8	50	14[a]	3/9	33
GH-162	6/16	38	GH-31[a]	4/7	57
622	6/16	38	3-1A-8-1	5/9	56
			TR-73	1/6	17
			GH-13	1/6	17
			14	1/4	25
			GH-417	2/3	67
			358	2/4	50
			GH-31	1/3	33
			GH-342	1/3	33

[a] Selfed plants

variation in transmission, it is proper to use a larger sample size in determining the transmission rate of the extra chromosome.

Transmission rates of the extra chromosome in relation to seed weight and germination percentage

Trisomics' seeds are mostly small, shrivelled, light in weight, and can be distinguished from bold and heavy seeds of normal disomics. The addition of one extra chromosome may affect the developmental phases of the plant. One effect can be poor development of the embryo and endosperm which results into the reduced weight of seeds. The relationship between seed weight and transmission rate of the seven trisomics is shown in Table 3.

Transmission rates of the extra chromosome tended to be much higher for small seeds than for heavy seeds for most of the trisomics. Based on seed weight, the maximum percentage of trisomics was recorded for light seeds in a selfed progeny of lax and the minimum in slender. Heavy seeds transmitted a very low percentage of trisomics in selfed progeny of dark green, slender and spindle. When trisomics were used as the female, the transmission of the extra chromosomes was maximal for light seeds in slender. Germination percentage was consistently lower for light seeds in each trisomic of pearl millet. This finding is in close agreement with those of Tsuchiya (1960) who divided seeds of two barley trisomics (bush and slender) into small and big classes, and observed a low percentage of germination in small seeds of both trisomics. Smaller seeds, however, yielded a higher percentage of trisomics in both cases. Liang (1979) also recorded a high percentage of plants with an extra chromosome grown from small seeds of certain trisomics of *Sorghum*.

Transmission rate of the extra chromosome in relation to plant size

The relationship between plant size and transmission rate is shown in Table 4. Most of the trisomic plants of

Table 3. Relationship among transmission rates, seed weights and germination percentages for seven primary trisomics in pearl millet

Trisomic type	Seed wt	Trisomics selfed			Trisomics × Disomics			Disomics × Trisomics		
		No. seeds tested	Germination %	Trisomics %	No. seeds tested	Germination %	Trisomics %	No. seeds tested	Germination %	Trisomics %
Tiny	Heavy	43	73.3	36.4	188	78.1	24.0	110	80.0	0
	Light	70	20.0	75.0	80	50.0	83.3	56	25.0	0
Dark green	Heavy	55	94.4	5.9	996	8.3	22.2	290	23.5	0
	Light	153	48.1	76.0	360	8.6	72.7	96	16.7	0
Lax	Heavy	337	25.9	20.0	573	30.2	20.7	423	27.4	0
	Light	617	3.9	85.7	124	25.0	80.0	120	8.3	0
Slender	Heavy	263	54.8	4.3	3 604	30.5	19.6	744	56.5	0
	Light	178	42.2	74.1	798	19.5	96.0	246	24.4	0
Spindle	Heavy	58	60.0	8.3	523	18.8	15.2	257	21.7	5.0
	Light	88	21.4	83.3	196	21.9	71.4	121	15.6	0
Broad	Heavy	225	77.6	27.1	569	48.4	14.0	398	39.1	0
	Light	104	25.0	75.0	215	27.9	84.2	90	20.0	0
Pseudonormal	Heavy	694	42.9	24.3	1 761	46.2	13.0	768	45.8	0
	Light	232	12.5	83.3	617	21.2	88.9	128	25.0	0

Note: Light seeds (1 000): test wt $(\bar{x}) = 2.8$ g, range = 2.0 to 4.8 g
Heavy seeds (1 000): test wt $(\bar{x}) = 5.0$ g, range = 3.6 to 6.1 g

Table 4. Relationship between transmission rates of the extra chromosome and plant sizes for seven primary trisomics in pearl millet

Trisomic type	Selfed trisomics			Trisomics as female			Trisomics as male		
	No. small plants	Trisomics		No. small plants	Trisomics		No. small plants	Trisomics	
		No.	%		No.	%		No.	%
Tiny	9	6	66.7	35	20	57.1	30	0	0
Dark green	30	18	60.0	25	12	48.0	20	0	0
Lax	18	8	44.4	35	15	42.9	34	0	0
Slender	30	10	33.3	260	95	36.5	120	0	0
Spindle	10	3	30.0	35	5	14.3	15	1	6.7
Broad	45	10	22.2	76	12	15.8	50	0	0
Pseudonormal	60	10	16.7	250	30	12.0	94	0	0
Total/average	202	65	32.2	716	189	26.4	363	1	0.3

Table 5. Transmission rates of the extra chromosomes, and pairing configuration and anaphase I distribution of chromosomes in seven primary trisomics of pearl millet

Trisomic type	Transmission rate when selfed (%)	No. of plants examined	Diakinesis and metaphase I cells (%)		Anaphase I cells (no.)				
			$7^{II}+1^{I}$	$6^{II}+1^{III}$	7-8	7-1-7	7-2-6	8-1-6	9-6
Tiny	23.3	15	22.9	77.1	144	3	–	–	–
Dark green	23.8	42	19.0	81.0	162	2	–	–	–
Lax	16.2	37	24.0	76.0	138	3	1	2	1
Slender	15.1	73	25.4	74.6	186	2	2	1	2
Spindle	16.7	18	25.5	74.5	204	4	2	–	1
Broad	16.4	67	21.9	78.1	126	5	–	2	–
Pseudonormal	13.8	109	30.7	69.3	244	8	2	1	–

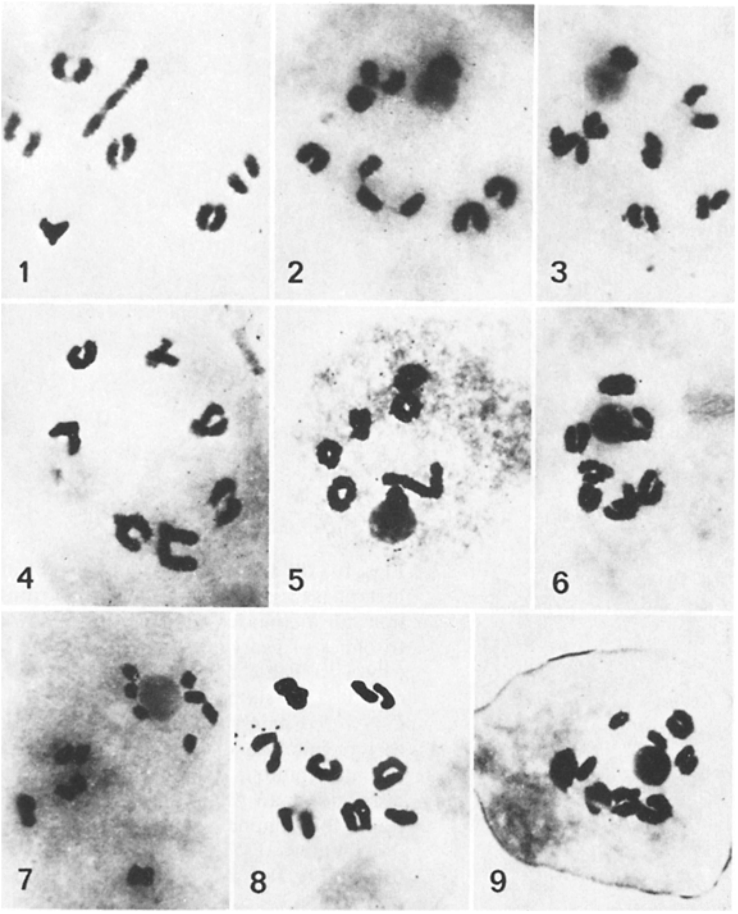
pearl millet showed reduced vigour and poor morphology. This may be attributed to the genetic imbalance caused by the addition of the extra chromosomes as the length of the extra chromosomes and the morphology of their corresponding trisomics are poorly associated in pearl millet (Gill et al. 1970; Nameeta 1973; Sai Kumar et al. 1982a). The correlation between small plant size and transmission rate was obvious for trisomics tiny, dark green, lax and slender (as both selfed and female parent). Small plant size did not seem to be related to the trisomic condition for pseudonormal in both classes of progeny. Liang (1979) also noted a high degree of correspondence between reduced plant size and transmission rate of *Sorghum* trisomics. Except in spindle male transmission was completely missing in most of the trisomics. However, sample sizes were relatively small for most of the trisomics, so variation due to small sample size should not be overlooked.

Relationship between transmission rate and behaviour of extra chromosome during meiosis

A significant and positive correlation ($r=0.758$) was measured between trivalent frequency and transmission rate. Univalents, however, showed a negatively significant association ($r=-0.758$) with the rate of transmission. The transmission rate and behaviour of the extra chromosomes during meiosis are presented in Table 5.

The extra chromosome in pearl millet trisomics may not always pair with its homologues but can remain as a univalent at diakinesis (Fig. 8) or it may pair with its homologues to form rod-, chain-, Y-, U-, L-, W-, pan- and V-shaped trivalents (Figs. 1–6, 10, 11, respectively). In certain PMC's, the three unpaired homologous chromosomes remained as 3^{I} (Fig. 9). The attachment of the trivalent to the nucleolus was noticed in certain cells of pseudonormal (Fig. 7). The frequency of chain trivalents was the highest followed by frying-pan or V-shaped trivalents. Other shapes of trivalents were relatively infrequent. There was a regular distribution of 7:8 at anaphase I and anaphase II (Figs. 15 and 18), and a few PMC's were noticed with one or two lagging chromosomes at anaphase I (Figs. 13, 14, 16). A low percentage of PMC's were seen with a 9:6 distribution of chromosomes at AI (Fig. 17).

After measuring the chromosome length, the somatic chromosomes of pearl millet were numbered

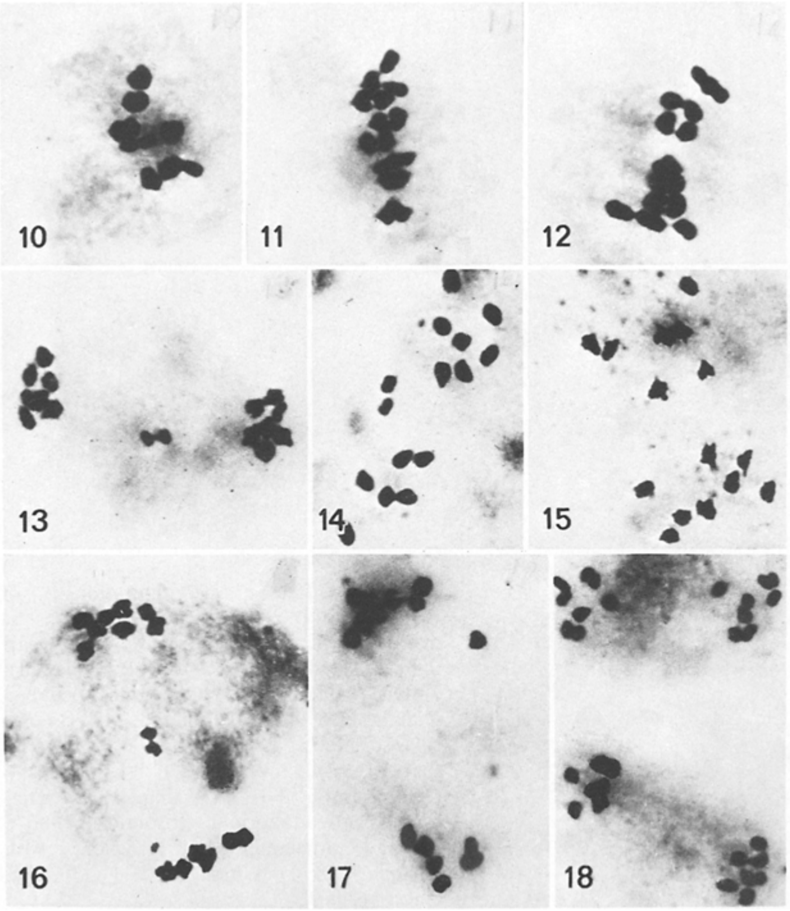


Figs. 1–9. Different configurations of trivalents and chromosome associations at diakinesis in primary trisomics of pearl millet. **1** Diakinesis, $6^{II}+1^{III}$ (Rod-shaped); **2** Diakinesis, $6^{II}+1^{III}$ (chain-shaped); **3** Diakinesis, $5^{II}+1^{III}$ (Y-shaped) $+\,1^{II}$ (Loosely associated); **4** Diakinesis, $6^{II}+1^{III}$ (U-shaped); **5** Diakinesis, $6^{II}+1^{III}$ (L-shaped); **6** Diakinesis, $6^{II}+1^{III}$ (W-shaped); **7** Diakinesis, 'pseudonormal' trisomic, $6^{II}+1^{III}$ showing attachment of trivalent with nucleolus; **8** Diakinesis, $7^{II}+1^{I}$; **9** Diakinesis, $6^{II}+3^{I}$

from 1 to 7 (Virmani and Gill 1972), which corresponds to trisomics, tiny, dark green, lax, slender, spindle, broad and pseudonormal, respectively. Chromosome length varied from 5.44 microns for the longest (first chromosome) to 3.20 microns for the shortest (seventh chromosome) (Virmani and Gill 1972). Trisomics tiny and dark green, involving the first and second chromosomes, respectively, showed a high frequency of trivalents and the maximum transmission rate of the extra chromosome. In contrast, pseudonormal (trisomic for the seventh chromosome) was associated with a maximum frequency of univalents and the lowest transmission of extra chromosome. In the case of a trivalent there is possibly less chance for the loss of an extra chromosome than when it exists as free univalent. A good correlation between chromosome length, trivalent formation and a high rate of trisomic transmission was noticed in maize trisomics (Einset 1943). The correlation between chromosome length and transmission rate was not apparent in tomato (Khush 1973) and *Lolium perenne* (Meijer and Ahloowalia 1981) although a high degree of correlation was noticed between trivalent frequency and transmission rate in trisomics of diploid alfalfa (Buss and Cleveland 1971). Though no straight forward relationship was apparent between chromosome length and trivalent formation, some association between trivalent formation and transmission rate was noticed in trisomics of *Avena strigosa* (Rajhathy 1975).

The relationship between transmission rate and gametic sterility

The maximum trivalent-forming trisomics, dark green and tiny were highly sterile. Minimum sterility was reported in pseudonormal where the trivalents were relatively less in proportion. It appears that longer chromosomes mostly form a trivalent and that univalents are frequent in those trisomics where the extra chromosome is the smallest one. Though trisomics involving longer chromosomes (tiny and dark green) showed a high degree of pollen and ovule sterility, they are highly transmissible, while the reverse is true with those associated with the smaller chromosomes in pseudonormal (Table 6). The correlation measured between genetic sterility and transmission rate is positive and significant ($r=0.851$, $P < 0.001$).



Figs. 10–18. Different trivalent shapes at metaphase I and chromosome distribution at anaphase I and II in primary trisomics of pearl millet. **10** Metaphase I, $6^{II}+1^{III}$ (Pan-shaped); **11** Metaphase I, $6^{II}+1^{III}$ (V-shaped); **12** Metaphase I, $6^{II}+1^{III}$ (Chain-shaped); **13** Anaphase I, early separation of univalent leading to 8:8 distribution; **14** Anaphase I, 7:2:6 distribution; **15** Anaphase I, 8:7 distribution; **16** Anaphase I, 8:1 (splitting):6 distribution; **17** Anaphase I, 9:6 distribution; **18** Anaphase II, 8:8:7:7 distribution

The trisomics showing high trivalent frequency and ovule sterility were highly transmissible although the reverse was true in minimum trivalent-forming trisomics such as pseudonormal. Nucleolar chromosomes are specially sensitive to abnormal conditions during meiosis (Arora 1978) and hence a low rate of transmission has been noticed in the case of pseudonormal trisomics of pearl millet. The trivalent frequency and viability of gametes seems to be affected by the length of the extra chromosome. The extra doses of longer chromosomes tend to cause more genetic imbalance, leading to a higher sterility of pollen and ovules. Thus, the transmission of trisomics in pearl millet seems to depend on the size of the extra chromosomes and on that of the relative frequency of the trivalents.

Relative importance of factors contributing to the transmission rate of extra chromosome

The value of R^2 reveals the total variation in the transmission rate due to the four contributing factors

Table 6. Relationship between transmission rate of an extra chromosome and pollen and ovule sterility in seven primary trisomics of pearl millet

Trisomic type	Transmission rate (as male) (%)	Plants examined (no.)	Pollen sterility (%)	Transmission rate (as female) (%)	Plants examined (no.)	Ovule sterility
Tiny	0	68	100.0	17.7	124	75.0
Dark green	0	56	86.5	18.4	76	78.0
Lax	0	84	97.0	14.7	136	70.0
Slender	0	320	75.2	14.4	836	65.0
Spindle	2.0	50	64.8	16.0	94	74.0
Broad	0	116	87.0	12.9	224	55.0
Pseudonormal	0	256	63.4	11.9	630	25.0

Table 7. Relative importance of the four factors contributing to transmission rates of the extra chromosomes as indicated by standard partial regression coefficients

Trisomics	R^2	Contributing factors and their standard partial regression coefficients			
		Plant size	Trivalent formation	Germination rate	Ovule sterility
Tiny	0.994*	4.69	-40.8	44.0	-6.86
Dark green	0.993*	1.04	0.11	-0.83	0.68
Lax	0.997*	0.46	-1.04	-0.41	2.90
Slender	0.999*	0.11	-0.19	-0.17	1.24
Spindle	0.996*	3.34	2.05	-0.73	-3.66
Broad	0.998*	0.81	-0.81	1.37	-0.36
Pseudonormal	0.995*	-2.36	-3.78	-1.96	9.06

* Significant at 1% level

which when combined contributed significantly to the transmission of all trisomics (Table 7).

Results of standard partial regression analyses indicate the relative importance of the four contributing factors to the transmission rates of the extra chromosomes (Table 7). Relative magnitudes of the standard partial regression coefficients indicate the relative importance of each contributing factor for each trisomic.

Genetic studies and the maintenance of trisomics depend on a combination of trisomic fertility and transmission rate of extra chromosomes. When individual chromosomes are added to the normal complement of a plant, the genetic balance is greatly disturbed. The disturbance is usually reflected in morphological and developmental deviations (Gill et al. 1970; Khush 1973; Nameeta 1973; Liang 1979; Sai Kumar et al. 1982a) and in biochemical pathways (McDaniel and Ramage 1970; Suh et al. 1976). The degree of disturbance seems to depend on the genetic content of the chromosome involved and the ploidy level of the plants. The polyploid species have a higher tolerance for aneuploidy (Palmer 1976). Trisomics in polyploids have normal or nearly normal morphology, fertility and vigour. They can tolerate the larger number of extra chromosomes, and transmission rates of extra chromosomes are near the expected. If such observations can be generalised, pearl millet should be considered a diploid because of (i) distinctive morphology of its trisomics (Gill et al. 1970; Nameeta 1973; Sai Kumar et al. 1982 a), (ii) the much lower transmission rate of the extra chromosomes than the expected 50%, (iii) the lack of identified monosomics and (iv) the absence of multivalents. The isolation of aneuploids higher than trisomics (Gill et al. 1970; Sai Kumar et al. 1981, 1982 b) and the occurrence of a few bivalents in haploid millet (Jauhar 1970 b), however, throw doubt on the true diploid nature of pearl millet. In addition, pearl millet has been considered to be a secondary-balanced diploid species (Jauhar 1968). It has also been reported that pearl millet is not a diploid species but that there has been duplication of chromosomes in its complement (Jauhar 1970 a).

Although five factors related to transmission rate were studied, other factors may contribute to the transmission rate of the extra chromosomes. The genic content of each chromosome could differ and thus affect the behaviour of the chromosome in meiosis and the frequency of transmission. Whether pollen with n+1 chromosomes germinates more poorly and whether their pollen tubes grow more slowly than those with n chromosomes should also be investigated.

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