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The Effect of Trisomy on Meiotic Behaviour of Interchange Complexes in Pearl Millet, *Pennisetum americanum* (L.) Leeke

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Summary. In the selfed progeny of a spontaneously produced triploid interchange heterozygote four different double trisomic plants were observed. In all the plants the frequency of alternate orientation of multivalents was lower compared to their respective types in the sib single trisomic plants. The frequency of alternate co-orientation of the interchange complex in these trisomics was also reduced compared to that of parental euploid disomic interchange heterozygotes. It is suggested that the presence of extra chromosomes influences the orientation behaviour of higher associations in different trisomics.

Key words: Meiotic behaviour – Trisomy – *Pennisetum americanum*

Introduction

In pearl millet there are a few reports on the cytology of single trisomics of various types (Gill et al. 1970; Manga 1976; Koduru et al. 1981), while Gill and Virmani (1971) reported double trisomics. Pantulu and Manga (1972) described the cytology of a plant with 16 chromosomes, in which the two extra chromosomes did not pair with the A chromosomes and formed an extra bivalent. In all probability these are closer to B chromosomes. In this paper we summarise meiosis in four types of double trisomics derived from a single source, with emphasis on the influence of trisomy on the metaphase I co-orientation of interchange complexes.

Materials and Methods

In the inbred line IP 457 a spontaneously occurring heterozygosity for an interchange was found to involve chromosomes 3 and 6; and was designated T3–6. The interchange in the homozygous condition produced a semi-dwarf phenotype (Koduru 1978, 1979). In the backcross progeny of the interchange heterozygote to the standard homozygote (IP 457), one of the 125 plants was a triploid. This triploid was selfed and in the progeny, 14 of the 93 plants were single trisomics ($2n+1=14+1$). These various types have been described earlier (Koduru et al. 1981). Four plants (T1–6, T2–2, T1–13 and T1–1) were double trisomics and the other 75 were diploids. Young spikes were fixed in acetic acid alcohol (1:3) for 24 h and stored in 75% alcohol until use. Acetocarmine stained squash preparations of PMCs were studied to analyse the meiotic behaviour.

Results and Discussion

Similar to the fourteen sib single trisomics reported earlier (Koduru et al. 1981) the four double trisomics also did not differ morphologically from the diploid plants. Gill et al. (1970) and Manga (1976) reported that the primary trisomics for chromosomes 1 to 6 of pearl millet differ from each other and also from the diploids in their morphology and therefore can be individually identified. Therefore, in our experimental line the phenotypic effects of the extra chromosomes are not expressed.

In the plants T1–6 and T2–2 two trivalents were formed in 41.98% and 75.05% of the PMCs respectively (Table 1, Fig. 1). In T1–6 all PMCs also carried one interchange association of four chromosomes. Thus T2–2 is regarded as a double trisomic (Fig. 1) and T1–6 as a double primary trisomic interchange heterozygote. At metaphase I non-disjunctional orientation of the trivalents and of the interchange association was prevalent (Table 2). The frequency of alternate orientation of trivalents is closely similar in the two double primary trisomic plants and is lower than that in the single primary trisomic plants (with or without interchange) reported earlier (Tables 3, 4, Koduru et al. 1981). The extra chromosomes in the two plants are not identified. Therefore it is not known whether the significantly lower frequency of alternate orientation of trivalents in the double trisomic plants is due to the

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Table 1. Chromosome behaviour at diakinesis in double trisomics of pearl millet ($2n+2=16$)

Plant no.	Total cells	Frequency of PMCs with[a]						Chiasma frequency
		$1_{III}+1_{V}$	$1_{III}+1_{IV}$	$2_{III}+1_{IV}$	2_{III}	$1_{III}+1_{IV}$	1_{III}	
T2-2	80	–	–	–	60	–	20	12.53±0.15
T1-6	81	–	–	34	–	47	–	12.79±0.23
T1-13	95	75	20	–	–	–	–	14.25±0.31
T1-1	83	21	–	–	46	9	7	13.61±0.21

[a] Only higher associations are given, others were bivalents and univalents

Table 2. Frequency of metaphase I co-orientation types of higher associations in double trisomics of pearl millet

Plant no.	Total associations	Trivalents			'Quadrivalents'			'Pentavalents'		
		Adj.	Alt.	Linear	Adj.	Alt.	Linear	Adj.	Alt.	Linear
T2-2	89	24	16	49	–	–	–	–	–	–
T1-6	186	25	16	51	32	19	43	–	–	–
T1-13	239	25	5	30	34	20	41	25	16	43
T1-1	149	33	3	31	6	3	11	18	8	36

Table 3. Percentile frequency of metaphase I co-orientation types of higher associations in euploid and aneuploid pearl millet

Ploidy	Trivalents			'Quadrivalents'			'Pentavalents'		
	Adj.	Alt.	Linear	Adj.	Alt.	Linear	Adj.	Alt.	Linear
$2n=14$[d]	–	–	–	51.75	48.25	0.00	–	–	–
$2n+1=15$[e]	15.44[a]	19.42	65.20	–	–	–	–	–	–
	10.78[b]	41.36	47.85	33.83	19.44	46.74	–	–	–
	26.95[c]	18.73	54.33	28.95	21.76	49.29	35.63	41.54	22.84
$2n+2=16$[f]	26.97	17.98	55.06	–	–	–	–	–	–
	27.17	17.39	55.43	34.04	20.21	45.75	–	–	–
	41.67	8.33	50.00	35.79	21.05	43.16	29.76	19.05	51.19
	49.25	4.88	46.27	30.00	15.00	55.00	29.03	12.90	58.07

[a] Primary trisomics; [b] primary trisomic interchange heterozygotes; [c] interchange trisomics; [d] Koduru (1979); [e] Koduru et al. (1981); [f] Present study

presence of an extra chromosome or due to the plants being trisomic for different chromosomes. However, irrespective of the plant being trisomic for a different chromosome, the interchange complex results from heterozygosity for chromosomes 3 and 6. The alternate orientation of the interchange complex in the double trisomic plant is significantly lower (20.20%) than the parental disomic interchange heterozygote (48.25%, Tables 3, 4, Koduru 1979). It is interesting to note that this low alternate orientation frequency of the interchange complex is not significantly different from that in sib single trisomic plants reported earlier (Koduru et al. 1981). Thus it appears that the presence of an extra chromosome influences the frequency of alternate orientation of the interchange complex. In view of the fact that the standard homozygous line (IP 457) and the interchange homozygote are being maintained for several generations (more than 15) by selfing individual plants all these lines are largely homozygous and isogenic, genetic differences between plants of different types are expected to be negligible. At anaphase I in both the double trisomic plants, only 8–8 and 9–7 chromosome segregation occurred, with the predominance of the latter type (61.84% and 63.24% respectively in the plants).

In plant T1-13, in addition to a trivalent an association of five chromosomes was present (Fig. 2). A normal trivalent was formed in all PMCs while the

Table 4. Comparison of M I co-orientation types of higher associations in euploid and aneuploid pearl millet

Genotypes	M I co-orientation types			Total	χ^2 (d.f. = 2)
	Adj.	Alt.	Linear		
Trivalents					
2n+1=15	113	141	214	468	32.40*
	(132.68)	(109.16)	(226.16)		
	107	40	161	308	
	(87.32)	(71.84)	(148.84)		
'Quadrivalents'					
2n=14	192	179	0	371	277.67*[a]
	(150.49)	(115.48)	(105.03)		
2n+1=15	139	75	231	445	
	(180.51)	(138.52)	(125.97)		
2n=14	192	179	0	371	204.94*[a]
	(168.87)	(141.36)	(60.77)		
2n+2=16	72	42	95	209	
	(95.13)	(79.64)	(34.33)		
2n+1=15	139	75	231	445	2.49
	(142.57)	(79.61)	(221.82)		
2n+2=16	72	42	95	209	
	(67.43)	(37.38)	(104.8)		
'Pentavalents'					
2n+1=15	81	105	58	244	56.22*
	(77.58)	(80.71)	(85.71)		
2n+2+16	43	24	79	146	
	(46.42)	(48.29)	(51.29)		

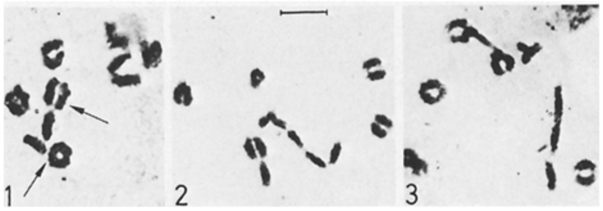
Expected values are given in parantheses

* χ^2 at 5% is 5.99

[a] χ^2 values, excluding the linear class, are 9.63, 4.58 respectively

association of five chromosomes or a quadrivalent and one univalent were formed in 78.95% and 20.05% of PMCs, respectively (Table 1). This suggests that this plant is a primary trisomic for one chromosome and an interchange trisomic for another. The chromosome behaviour at diakinesis showed that of the three possible post pachytene configurations suggested for an interchange trisomic (Sybenga 1972) only the above two were realised. It may be noted that in the sib single interchange trisomics all three types were realised (Koduru et al. 1981). At metaphase I the frequency of alternate orientation of the primary trisomic trivalent is much lower (8.33%) than that in T2–2 and T1–6 while that of the 'quadrivalent' derived from the interchange complex is in agreement with that observed in T1–6 indicated above. Among the pentavalents, 19.05% showed alternate orientation (Table 2). Again this frequency is much lower than that of sib single interchange trisomics studied earlier (Tables 3, 4). At anaphase I 76,47% of the PCMs showed 9–7 chromosome distribution and the others showed 8–8 distribution.

The fourth plant T1–1 is primary trisomic for one chromosome and tertiary trisomic for the other (Fig. 3). As in T1–13, the primary trisomic trivalent is formed in all the PCMs while only 25.30% of PMCs had the pentavalent of the tertiary trisomic. However, in the sib single tertiary trisomics (which did not carry the additional trisomic) pentavalents were formed in 62.05% of



Figs. 1–3 Meiosis in double trisomics of pearl millet (bar represents 10 µm). **1** Diakinesis in a double primary trisomic. Two frying pan type trivalents are indicated by arrows. **2** Diakinesis with one primary trisomic trivalent and one interchange trisomic pentavalent. **3** Diakinesis with one primary trisomic trivalent and one tertiary trisomic pentavalent

the PMCs (Koduru et al. 1981). The other types of associations seen were given in Table 1. The critical dumb-bell shaped configuration expected for a tertiary trisomic is seen in 23.81% of pentavalent forming PMCs (the frequency of such critical configuration in the sib single tertiary trisomics is 16.66% of pentavalent forming PMCs). The orientation behaviour of various higher associations at metaphase I resembled T 1–13 (Table 2). First anaphase cells showed a 9–7 distribution in 85.53% of them.

In the four double trisomics unequal anaphase I chromosome segregation constituted the majority. All the plants were completely male and female sterile. These evidently show that the observed numerically balanced (8–8) chromosome segregation at anaphase I in a reasonable per cent of PMCs did not lead to genetic balance in the haploid gemetes. This infers that the pearl millet genome may be capable of maintaining aneuploidy at the haploid level only rarely.

A comparison of the metaphase I orientation behavior of the interchange complex and the other higher associations of the aneuploid genomes with that in the euploid genome reveals a reduction in the per cent alternate orientation (Tables 3, 4), suggesting chromosomal effects on the events. This is consistent with the genetic control of co-orientation frequencies of an interchange complex reported earlier in this species (Koduru 1979).

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