Origin and Meiotic Behaviour of Two Multiple Interchange Trisomics in Pearl Millet (*Pennisetum americanum* L. Leeke)

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Chromosomal aberrations like interchanges and translocations are useful cytogenetic tools which have been utilized extensively in crop improvement programme. They are also important from the evolutionary point of view as they are known to bring about karyotypic changes which in the long run may have some adaptive advantages over natural populations. Chromosomal interchanges, both induced and spontaneous origin, have been reported in pearl millet (Powel and Barton 1969, Jauhar 1974, Tyagi 1976). Interchange trisomics have been reported by Manga (1977), Minocha and Barr (1976), Rao *et al.* (1977), and others. In the present study the origin and meiotic behaviour of two multiple interchange trisomics have been discussed.

Materials and methods

The two multiple interchange trisomics ($2n=15$) were isolated in the progeny of two tertiary interchange trisomics which in turn were obtained from some of the primary trisomics reported earlier (Vari and Bhowal 1986). The plants were raised in pots along with normal diploids and trisomics. For meiotic studies young spikes were collected and fixed in 3:1 alcohol acetic acid and slides were made by the usual acetocarmine staining method.

Results

Origin and morphology

The parental trisomics from which the multiple interchange trisomics were isolated were tertiary interchange trisomics as they showed in diakinesis a chromosome association of $1^V + 5^{II}$ or $\odot 4 + 5^{II} + 1^I$. The multiple interchange trisomic designated as 29-2 had all the chromosomes while the other 31-7 had at least seven chromosomes involved in translocation. The other sister plants were either tertiary trisomics, tertiary interchanges or diploids with translocations.

The two multiple interchanges differed from the disomics as well as the other trisomic types in their morphological characters. They were short in stature, less vigorous with slender stem and narrow short stiff leaves having profuse hairs on the lamina and petiole. They flowered very late compared to disomics and parental trisomics.

Cytology

The frequency of different type of chromosome association at diakinesis is given in Table 1. In 29-2 association involving all the fifteen chromosomes were observed occasionally (Fig. 1) indicating that it is a multiple interchange trisomic which involved all the chromosomes. In 31-7 the maximum number of chromosomes involved in translocation was seven as it showed a

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Figs. 1-6. Chromosome associations at diakinesis in multiple interchanges. 1, 2, Multivalent involving 15 chromosomes in 29-2. 3, 1^{III}+6^{II} association in 29-2. 4, 1^{IX}+3^{II} association in 29-2. 5, Bivalents showing interconnections in 29-2. 6, 1^{VII}+4^{II} association in 31-7.

chain of seven chromosomes (Fig. 6). In both the interchanges the most common type of association observed was 1^{VII}+4^{II}. In 27-2 associations like a 7+4^{II}, 5+5^{II} and 1^{IX}+3^{II} (Fig. 4) were also observed.

In 29-2 very often at diakinesis when bivalents were present they tend to show some interconnections (Fig. 3). Very often varying number of bivalents were found attached to the multivalents (Figs. 2 and 4) or the bivalents were found to be in groups of 2 or 3 with interconnections (Fig. 5). Out of 115 PMCs studied critically only one case was found in which all the seven bivalents remained separate.

The multivalent formation in the interchanges resulted in varying types of abnormalities in later stages of meiosis (Table 2). Only about 50% of the PMCs showed normal 7/8 anaphase disjunction. PMCs having one or two laggards, 9/6 disjunction were quite common in both the interchanges. Tetrads with micronuclei varying from 1 to 4 were observed in about 25% of the cells. The pollen fertility was reduced to 39.39% in 29-2 and 45.58% in 31-7. The seed fertility was very low in both interchanges as

Table 1. Chromosome associations at diakinesis in multiple interchange trisomics

Type of chromosome association	% of cells in 29-2	% of cells in 31-7
1 ^{XIV} + 0 ^{II}	1.70	0
1 ^{VII} + 4 ^{II}	46.35	46.08
1 ^V + 5 ^{II}	26.83	20.08
1 ^{IV} + 4 ^{II}	21.96	0
1 ^{III} + 6 ^{II}	2.43	26.00
7 ^{II} + 1 ^I	2.43	6.15
PMCs studied	164	115

Table 2. A-1 disjunction in multiple interchange trisomics

Type of disjunction	% of cells in 29-2 interchange	% of cells in 31-7 interchange
7-8	50.0	57.3
7-1-7	22.8	6.5
7-2-6	6.4	10.0
9-6	14.8	23.5
8-1-6	6.0	—
No. PMCs studied	250	200

they produced only 10–15 seeds in few of the panicles.

Discussion

Multiple interchanges involving all the chromosomes have been induced in diploid pearl millet by various authors. Minocha and Brar (1976) produced a multiple interchange trisomics involving seven chromosomes by intercrossing two interchanges. In the present study multiple interchange trisomic involving all the fifteen chromosomes were obtained in the progeny of a tertiary interchange trisomic suggesting that aneuploidy (trisomy) with translocation could induce further chromosome alterations in *Pennisetum americanum*.

Structural changes associated with aneuploidy has been reported as early as 1928 by Belling and Blakeslee in *Datura*. Subsequently in crop like *Zea* (Clark and Copeland 1940), *Lilium* and *Hyacinthus* (Brock 1954 and 1955), *Trillium* (Rutishauser 1956) etc. and it has been shown that translocations occur more frequently in triploids than in diploids. Ising (1969) in *Cyrtanthus* observed that aneuploidy especially trisomics of species hybrids are more effective in producing new chromosomal changes. Several theories have been put forward as the cause of the spontaneous chromosome alteration in aneuploids as well as in diploids. Chromosome breakage in aneuploid may be due to the genetic imbalance caused by certain automutagenic substance or due to the deficiency of radical substances (Heneen 1963).

In *Cyrtanthus*, Ising (1969) observed that certain trisomics give higher frequency of breakages which he suggested may be due to several duplicated segments or they may generate more automutagenic substances which may be necessary for primary single strand breaks. It may be suggested that whatever the cause of chromosome breakage in aneuploids of a crop like *Pennisetum*, aneuploidy together with translocations of spontaneous nature could produce structural changes in chromosomes and could alter the basic karyotype that may be important on the evolutionary point of view.

The meiotic behaviour especially the chromosome associations in the multiple interchange 29–2 was found to be of interest. Though from Fig. 1 and 2 it is evident that all the chromosomes in the complement was involved in translocation the frequency of cells having this type of association was very low. The high frequency of PMCs having $1^{VII}+4^{II}$ type association indicates that very often only seven of the interchanged chromosomes could take part in pairing and others remained separate to form bivalents. Also it was interesting to note that though there was possibility of forming more than one multivalent per cell only one multivalent per cell was present except in cases where one quadrivalent and one trivalent per cell was observed. Another observation peculiar to 29–2 was the secondary associations or interconnections between the bivalents observed. Secondary association of chromosomes has been reported in many of the diploid species and it has been interpreted as the result of modified chromosome rearrangement such as duplication, interchange etc. by Stebbins (1950), Darlington (1928), Darlington and Moffot (1930). Lawrence (1931) and Riley (1960) consider it as direct evidence of remote affinity between chromosomes. In the present study it may be suggested that complete homology between chromosomes resulted in bivalent formation and the interconnections between bivalents represents segmental homology due to interchanges. It may be possible that the genetic homology between some of the interchanged chromosomes may not be sufficient enough to ensure complete pairing and early terminalization of chiasma has taken place and they remained as bivalents but still maintaining their affinity to the multivalent or to other bivalents.

In earlier studies involving multiple interchanges high frequency of cells having multivalents have been observed. Sukdev *et al.* (1985) reported a maximum association of 10 chromosomes in about 66.3% cells in a multiple interchange of *Pennisetum*. In induced seg-

mental interchanges of *Pennisetum* Lal and Srinivaschar (1979) observed almost 100% of the PMCs with quadrivalents or higher multivalents. It may be suggested that multiple interchanges with reduced frequency of multivalents per cell may be more advantageous as they may show less abnormalities in later stages of meiosis which in turn could reduce the gametic sterility.

Summary

Two multiple interchange trisomics one involving all the fifteen chromosomes and other at least seven chromosomes were isolated in the progeny of two tertiary interchange trisomics of pearl millet (*Pennisetum americanum* ($2n=14$)). The study of chromosome association of diakinesis in these multiple interchanges showed varying frequencies and type of multivalent formations followed by abnormalities in later stages of meiosis. Secondary association of bivalents was quite frequent in one of the interchange. Aneuploidy together with translocation as the probable cause of further chromosome interchanges has been discussed on the light of the present investigation.

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