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Review

Cytogenetics of Pearl Millet

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Contents

Summary. The somatic karyotype of pearl millet *Pennisetum americanum* (L.) Leeke. (2n = 14) has been studied in several cultivars, but few cytological markers have been discovered which could help in the easy identification of the chromosomes. Analysis of pachytene bivalents permits such identification but is feasible only in a few cultivars. Recently, several lines having telocentric chromosomes have been produced and classified but their potentialities as cytogenetic tools have yet to be explored. Some African populations of pearl millet carry B-chromosomes in their karyotype. Cytogenetics of B-chromosomes has been reported in great detail. Bs undergo spontaneous changes to produce deficient- and iso-chromosomes. The main effect of B-chromosomes is on chiasma frequency which is exerted by the relative amounts of chiasma promoting euchromatin and the chiasma depressing heterochromatin in the Bs. Haploid plants occur occasionally and sometimes show a low degree of seed set, offering a possibility of establishing homozygous inbred lines. Cytogenetics of several spontaneous and induced autotetraploids have been reported. In general quadrivalent formation between the seven sets of four homologues was random. Seed set of the autotetraploids could be improved by selection; improved seed fertility was found to be associated with increased chiasma frequency, increased quadrivalent frequency and regular distribution of chromosomes at anaphase I. Genes controlling morphological characters of plant phenotype segregate independent of those controlling fertility and in pearl millet polyploidy per se is not limiting to plant vigour. Primary trisomics represent the best studied among the aneuploids of pearl millet. All the seven primary trisomics have been identified and described. Some were used in assigning genes to specific chromosomes but in general trisomics have poor vigour and fertility, and show low frequency of transmission. Apart from B-chromosomes, cytogenetics of interchanges has been the best studied aspect of pearl millet. The frequency of co-orientation of an interchange complex at metaphase I, which determines the fertility or sterility of the interchange heterozygote, is influenced by the genetic background and thus is theoretically amenable

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for selection leading to improved fertility of the heterozygote. Interchange tester-stocks have been assembled which can be used to identify the chromosomes involved in any newly obtained interchange. A complex interchange line involving all the chromosomes of the complement has also been produced, but the ring-of-fourteen produces total male and female sterility.

Genotypic control of mitosis and meiosis has been reported, with reference to chromosome numerical mosaicism, multiploid sporocytes, desynapsis and chromosome fragmentation, and male sterility. Pearl millet being a largely outbreeding species, forced inbreeding was mainly found to result in loss of morphological vigour and reduction in mean chiasma frequency per PMC. Interspecific hybrids between pearl millet and several related species have been cytologically investigated and homology of the seven chromosomes of pearl millet with seven of the fourteen chromosomes of *P. purpureum* has been demonstrated. Cytogenetic evidence from haploids, autopolyploids and interspecific hybrids has indications to suggest that the haploid number of x = 7 is derived from x = 5, but the evidence is inconclusive and needs critical evaluation.

Key words: Pearl millet – *Pennisetum americanum* – Cytogenetics

1 Introduction

Pearl millet, *Pennisetum americanum* (*L.*) *Leeke,* is an important cereal crop in India and in several African countries. In terms of annual production, pearl millet is the sixth most important cereal crop in the world; among millets it ranks next to *Sorghum* (Brunken et al. 1977). It occupies 11 million hectares in India as compared to the world area of 20 million hectares and forms the staple diet of an estimated 10% of the Indian population (Gupta 1977). Nutritionally the grain of pearl millet is higher than wheat, rice or corn in fat and mineral content (particularly calcium and iron content) and is similar in other constituents (Burton and Powell 1968). The cytogenetics of this crop species, mainly the information published since 1968, is reviewed here; for a review of the earlier literature reference may be made to Burton and Powell (1968).

2 Karyomorphology

2.1 Somatic Karyotype

The somatic karyotype of pearl millet (2 n = 14) consists of two or three metacentric chromosome pairs, two or three sub-metacentric pairs and one or two acrocentric pairs (Pantulu 1961). In some varieties of African origin one or two of the longer pairs reveal secondary constrictions in their long arms. It is now generally accepted that the shortest chromosome pair of the complement carries the nucleolar organiser in the short arm. Chandola and Jain (1970) described considerable karyotypic variation in pearl millet varieties. Significantly, they reported three telocentric pairs in the varieties of Sudanese origin. Though telocentric chromosomes can be maintained by selfing (Pantulu and Rao 1977 a), it is doubtful whether they would survive in nature since pearl millet is a highly cross pollinated species.

Considering the various detailed analyses of the somatic karyotype (Sree Ramulu and Sree Rangasamy 1971; Virmani and Gill 1972; Tyagi 1975 a) it is clear that the chromosomes no doubt differ in length and arm ratios, but the differences are hardly sufficient to permit a ready and reliable identification of the individual chromosomes under a microscope, except for the nucleolus organizing chromosome. Even Giemsa C-banding of the somatic chromosomes was not useful for the purpose (Pantulu et al. 1978).

2.2 Pachytene Chromosome Morphology

The morphology of pachytene bivalents of pearl millet was described by Pantulu (1958) and Venkateswarlu and Pantulu (1968) in 'AKP 3' and by Lobana and Gill (1973) in 'BIL 4'. There are differences in the arm ratios for some of the chromosomes between the two varieties. Further, in 'AKP 3' a good correlation between pachytene and somatic karyotypes was observed, whereas in 'BIL 4' such a correlation was not evident. This difference probably stems from the relative abundance of heterochromatin in 'BIL 4' and its limited occurrence in 'AKP 3'. In view of the regulatory role of extra heterochromatin on chromosome pairing and chiasma formation, a survey of pearl millet varieties from different Agro-ecological regions is desirable. Moreover, Pantulu et al. (1978) suggested the possible occurrence of two types of heterochromatin at the centric regions.

2.3 Telocentric Chromosomes

There are several reports of occurrence of telocentric chromosomes in pearl millet (Srinivasachar and Lal 1971; Narasinga Rao 1977; Narasinga Rao et al. 1977; Pantulu and Rao 1977 c; Sukhadev et al. 1979). However, most of these are unstable genotypes. The selfed progenies of such plants vary in their genome constitu-

tion and in some instances the telochromosomes in the progenies were unrelated to the telocentrics in the parents. However, occurrence of a stable new karyotype, $2n = 12 + 4$ telo, was reported by Pantulu and Rao (1977a). The four telocentric chromosomes represent a homologous pair of normal chromosomes and hence the karyotype was genetically balanced; the telocentrics could be maintained through selfing for over ten generations. Rao (1980) made a detailed study of telocentrics for chromosomes 1 and 7, classified 20 different aneuploid types and proposed a standard nomenclature for them. Broadly he recognised 1) substitution diploids, which are aneuploids with telocentrics substituting one, two or more chromosomes in the complement, 2) single arm, or 3) two arm addition types, 4) telo plus full chromosome additions and 5) monosomics for one arm.

3 B-Chromosomes

3.1 Occurrence

B-chromosomes are known only in pearl millet populations of African origin (Pantulu 1960; Powell and Burton 1966, Burton and Powell 1968). Some of the B-chromosomes exhibit nucleolus organising activity.

3.2 Morphology, Cytological Behaviour and Inheritance

At somatic metaphase B-chromosomes are distinctly smaller than the A-chromosomes and usually remain at the periphery of the metaphase plate in root tip cells. Pantulu (1960), Venkateswarlu and Pantulu (1970) and Powell and Burton (1966) reported variation in the number of Bs per cell between different plants and also between different cells of a root tip and an anther.

The accessories studied by Powell and Burton (1966) were euchromatic with median centromeres. On the other hand the B-chromosomes originally described by Pantulu (1960, 1961) had subterminal centromeres flanked by heterochromatin. The short arm was completely heterochromatic and the long arm had proximal heterochromatin followed by a euchromatic region with eight chromomeres. Subba Rao and Pantulu (1978) subsequently designated them as Standard Bs, to distinguish them from derived Bs with different morphology designated as Deficient and Iso-Bs. Comparison of pachytene morphology revealed that the Deficient B-chromosome was related to the Standard B by the deletion of a part of the euchromatic segment carrying two chromomeres and the Iso-B was an isochromosome of the long arm of the Deficient B.

The cytological behaviour of the Standard B chromosomes in their original genetic background of the Sudanese stock was studied by Pantulu (1960, 1961) and Venkateswarlu and Pantulu (1970) while Pantulu and Manga (1975) studied them in the genetic background of an Indian inbred line. Cytogenetics of the derived Bs was investigated by Subba Rao and Pantulu (1978). In all the genetic backgrounds B-chromosomes never paired with A-chromosomes but paired only among themselves, forming bivalents and multivalents. Pantulu (1960) observed that, at pachytene, synapsis involved both the eu- and heterochromatic segments, but at later stages chromosome associations by chiasmata were confined to euchromatic segments alone.

Subba Rao and Pantulu (1978) reported that when appropriate number of Bs were present, Iso-Bs showed highest bivalent and multivalent frequencies while Deficient Bs showed the lowest frequencies. They also reported pairing among the three types of Bs when they were present together, indicating the homology of their euchromatic portions. Most frequently (69%) Standard and Deficient Bs paired, while Standard and Iso-Bs paired less frequently (61%); in only 49.5% of the cases all the three types of Bs were associated. Pairing between Iso- and Deficient Bs was also noticed when they were present together.

Large, small and intermediate sized Bs were also observed in Inbred 227 studied by Powell and Burton (1966). The large accessory appears to be an isochromosome derived from the intermediate-sized accessory chromosome.

Pantulu and Manga (1975) studied the chiasma frequencies for Standard B-chromosomes and reported an increase in the mean chiasma frequency as well as an increase in the variance of the mean with increasing number of Bs. These effects were evident only when the Bs were present in the Indian inbred line but not in their original Sudanese line, which is suggestive of the influence of A-chromosome genotype on the behaviour of B-chromosomes.

Subba Rao and Pantulu (1978) reported that in plants with standard, Deficient or Iso-Bs in corresponding numbers, the mean chiasma frequencies of Iso-Bs were higher than those of Standard or Deficient Bs. The mean chiasma frequencies of Standard and Deficient Bs were not significantly different except in the 4B classes. In the case of Standard and Deficient Bs there was a positive correlation between the B-chiasma frequency and B-chromosome number. Such a correlation was not observed in the case of Iso-Bs. A comparison of the variances of the mean B-chiasma frequencies between plants revealed that in the 2B class the variance of Iso-Bs was significantly higher than that of Deficient Bs but not different from that of Standard Bs. In the 3B and 4B classes the variances differed as Standard > Deficient > Iso-Bs.

The effect of A-chromosome genotype, particularly of the desynaptic gene, on the behaviour of B-chromosomes was studied by introducing Standard and Deficient Bs into desynaptic genetic background. The Bs in desynaptic background never formed multivalents; the frequency of bivalents also was reduced. The effects of the desynaptic gene on chromosome associations and chiasma frequencies were similar on both B- and A-chromosomes (Pantulu and Subba Rao 1976).

Chromosome non-disjunction at anaphase I and precocious division of Bs during PMC meiosis were reported by Pantulu (1961).

Pantulu (1961), Subba Rao and Pantulu (1978) and Subba Rao (1980a) reported that the transmission of the three types of Bs varied in the reciprocal crosses. Further, all the three types exhibited slight accumulation in the progeny when transmitted through seed parent. The transmission frequency of the Deficient and Iso-Bs through the male parent differed markedly from that of the Standards. The Standard Bs showed a slight gain while the Deficient and Iso-Bs showed considerably reduced transmission through the male line and consequently there was some loss of these two types of Bs. The higher frequency of transmission of Deficient and Iso-Bs

through the female than through the male might be due to directional segregation of Bs into the functional megaspores. The slight increase of Standard Bs in the progeny when transmitted through the male parent might be due to chromosomal non-disjunction as reported by Jayalakshmi (unpublished) at the second mitotic division in the pollen grain and preferential fertilization.

3.3 *Effects of B-Chromosomes*

The effects of the three types of B-chromosomes on A-chromosome chiasma frequencies were studied by Pantulu and Manga (1975) and Subba Rao and Pantulu (1978). A single standard B had no effect while two or three Bs produced a significant increase, but more Bs reduced the mean A-chiasma frequency to the level of the 0–B cells. Therefore, when all the Standard B classes were considered together the Bs showed no effect on mean A-chiasma frequency.

One to two Deficient Bs had no effect on the mean A-chiasma frequency but three or four Bs had a depressing effect. There was a significant negative correlation between Deficient B-chromosomes and mean A-chiasma frequencies.

There was an increase in the mean A-chiasma frequency when one to four Iso-Bs were present when compared with 0–B plants, but the increase was not proportional to the number of Iso-Bs. There thus seems to be a threshold value for the effect of the Iso-Bs.

Subba Rao and Pantulu (1978) compared the effects of Standard, Deficient and Iso-Bs when present in corresponding numbers. They reported that in most cases the plants with Iso-Bs had higher mean A-chiasma frequencies than those with Standard or Deficient Bs, and plants with Deficient Bs had significantly lower mean A-chiasma frequencies than plants with Standard Bs except in the 1 B class. Thus Iso-Bs bring about an increase and Deficient Bs bring about a decrease while the Standard Bs have no effect on the mean A-chiasma frequencies.

The combined influence of the three types of Bs was studied by Subba Rao and Pantulu (1978) by comparing the effect produced when Iso, Standard and Deficient Bs were present together in the same PMCs in different combinations, with the effect produced when corresponding numbers of each type of Bs were present separately. The effects of different types when present together were remarkably close to the means of the values obtained when the two or three types were present separately in corresponding numbers.

Powell and Burton (1966) found no relationship between the number of accessories and A-chromosome pairing in their material. However, they reported the existence of a relationship between associations of accessories and pairing of the A-chromosomes.

Pantulu and Manga (1975) and Subba Rao and Pantulu (1978) investigated the effect of Bs on the variance of mean A-chiasma frequency and reported, for Standard and Deficient Bs, a positive correlation between B-number and variance of the mean A-chiasma frequencies. Iso-Bs had a slightly different effect in that the mean A-chiasma variance in all B-classes (one to four Iso-Bs) was more or less similar and significantly higher than that of 0–B plants. When the variances of mean A-chiasma frequencies in plants with various combinations of the three types of Bs were compared with plants having any one type of Bs in numbers equal to the total in combination, all showed significantly lower values.

The chiasma frequencies of A and B chromosomes, as reported by Pantulu and Manga (1975) and Subba Rao and Pantulu (1978) were not interdependent and hence were judged to have no mutual interference.

According to Subba Rao and Pantulu (1978) the effects of the three types of Bs on mean A-chromosome chiasma frequency per cell present a complex situation. The Deficients have the same amount of heterochromatin as the Standards but unlike the Standards, three or more Deficient Bs depress the mean; the Iso-Bs on the other hand have reduced heterochromatin and show an enhancing effect on the mean. They explained this situation by assuming that the euchromatic long arm of B-chromosomes brings about an increase in the mean cell A-chiasma frequency, while the heterochromatin of the B has a depressing effect on the mean; consequently the loss of heterochromatin results in the loss of the depressing effect and leads to an increased mean. The relative amounts of eu- and heterochromatin in them seem to be responsible for the varying effects produced by the different types of B-chromosomes.

B-chromosomes also influence the meiotic behaviour of A-chromosomes. Pantulu and Manga (1975) and Subba Rao and Pantulu (1978) observed in some plants with four or more Standard or Deficient Bs differential condensation of chromosomes, desynapsis and persistent nucleoli. In plants with two Iso-Bs, A-chromosome nondisjunction occurred in two per cent of the PMCs at anaphase I, and in their selfed progeny the expected trisomics were found.

Krishna Rao et al. (1979) observed that three Standard B-chromosomes had very little effect on the duration of the mitotic cycle whereas five B-chromosomes resulted in an increase of the duration by about 39%. This effect closely paralleled the depressive effect of Bs, when present in larger numbers, on the general vigour of the plant, on fertility and meiotic behaviour of A-chromosomes reported by Pantulu and Manga (1975).

Pantulu (1961) studied the effect of Standard Bs on exophenotypic characters in the original Sudanese stock while Manga (1972) studied their effects in an Indian inbred line. Manga observed in all morphological characters a general increase in the mean values and variances when one to three Bs were present, but a depressing effect when four or more Bs were present. On the other hand, in the Sudanese line the Bs in smaller numbers had a slight stimulating effect on the vegetative characters and general vigour but in larger numbers they were neutral. This variable effect of Bs was partly attributed to the interaction between the B- and A-chromosome genotypes.

Pantulu and Manga (1975) observed little loss of pollen fertility when one to four standard Bs were present; but with a greater number of Bs fertility was very much reduced. This reduction may partly be due to a decrease in chiasma frequency of A-chromosomes and desynapsis leading to univalent formation and the irregular distribution of univalents. The high or complete sterility observed in five or more Standard-B classes may not entirely be due to meiotic abnormalities for

two reasons. Firstly, the failure of the anthers to dehisce, a condition associated with the sterility, might be genetically controlled. Secondly, the frequency of PMCs with univalents was comparatively lower than the amount of sterility observed.

4 Haploids

Haploid plants in pearl millet were recognized by several investigators (Pantulu and Manga 1969; Jauhar 1970b; Manga and Pantulu 1971; Gill et al. 1973; Powell et al. 1975). Though occasionally haploid plants have been observed among twin seedlings produced by polyembryonic caryopses (Pantulu and Manga 1969; Manga and Pantulu 1971; Powell et al. 1968, 1975), Powell et al. (1975) observed that polyembryony is not a very active force in the production of haploid plants in pearl millet.

All investigators reported the occurrence of two to three bivalents in the haploids at diakinesis or metaphase I. Jauhar (1970b) observed up to two bivalents per cell, some with interstitial chiasmata, and considered them as evidence for a basic number of five for pearl millet. However, Pantulu and Manga (1969) and Manga and Pantulu (1971) observed that the frequency distribution of bivalents at metaphase I followed a truncated Poisson distribution suggesting that the bivalents were random pairs. They considered them to be pseudobivalents and not indicative of a lower basic number than seven. Gill et al. (1973) considered that the bivalents were the result of segmental homologies among some chromosomes whereas Powell et al. (1975) concluded that the pairing of chromosomes in pearl millet haploids was indicative of duplicate loci or a marked tendency for non-homologous pairing.

Some amount of end-to-end (e-e), side-to-side (S-S) and end-to-side (e-s) types of associations were observed among the univalents as well (Pantulu and Manga 1969; Manga and Pantulu 1971, Gill et al. 1973). Pantulu and Manga showed that these associations were also random pairs exhibiting truncated Poisson distribution like the bivalents.

The haploids observed by Powell et al. (1975) showed large seed set, which they believed was a result of the combined effect of the formation of balanced gametes, from the 0–7 distributions at anaphase I, and of the tendency for spontaneous doubling of chromosome number in the haploids. The fertility of the haploids opens up the possibility of establishing homozygous inbred lines in pearl millet.

5 Autotriploid

Krishnaswamy and Rangaswami Ayyangar (1941) were the first to report an autotriploid pearl millet (in the progeny of X-ray irradiated seed). They observed higher associations of rings of four, and chains of six and ten chromosomes, in addition to trivalents.

Pantulu (1968) studied in detail a triploid obtained from gamma ray irradiated seed. Morphologically the plant differed from the normal diploid in having lateral branching and profuse tillering. The chiasma frequency in the triploid was one and half times that in the diploid. Frequent formation of seven trivalents, with a mean trivalent frequency of 6.18 at metaphase I, was observed.

One triploid obtained by colchicine treatment (Manga 1972) was reported to have a lower chiasma frequency and lower trivalent frequency compared to the triploid studied by Pantulu (1968).

6 Autotetraploids

6.1 Cytology and General Account

Tetraploidy in pearl millet was first induced by Krishnaswamy et al. (1950) by colchicine treatment of diploid seedlings. Gill et al. (1966), Jauhar (1970a) and Minocha et al. (1972) also obtained tetraploids by the same method. The tetraploids were poor in vigour though they possessed some gigas characters. Spontaneous origin of tetraploids has also been reported (Powell and Burton 1968; Hanna et al. 1976; Kodura and Krishna Rao 1978). Crossing of tetraploids and diploids was often unsuccessful but occasional formation of triploids was reported by Gill et al. (1969) and Jauhar (1970a). Reversion to diploidy in selfed and open pollinated tetraploids was reported to be frequent (Table 1). Gill et al. (1969) observed association of 5, 6, 7 and 9 chromosomes while Jauhar (1970a) reported associations of 5, 6 and 8 chromosomes at a low frequency up to the C_3 and C_4 generations of the tetraploids. Hanna et al. (1976) reported occurrence of high frequency of tetraploids in polyembryonic and non-polyembryonic inbred 'Tift-239'. They contended that one of the factors accounting for the poor seed set of the tetraploid was production of unbalanced gametes due to multivalent chromosome pairing. Singh et al. (1977b) obtained a tetraploid after gamma ray treatment of diploid seed; they reported only bivalent associations of chromosomes in the PMCs and total sterility.

6.2 Fertility

Gill et al. (1969), Jauhar (1970a) and Minocha et al. (1972) observed increased fertility (seed set) in the advanced generations of autotetraploids, which they

Table 1. Comparison of cytogenetic characters of autotetraploid pearl millet from different sources

	Raman et al. 1962	Gill et al. 1969	Jauhar 1970a; Jauhar et al. 1976	Hanna et al. 1976	Koduru and Krishna Rao 1978	Narasinga Rao 1978; Arundhati 1980
1. Origin	Colchicine induced	Colchicine induced	Colchicine induced	Spontaneous	Spontaneous	Colchicine induced
2. Mean quadrivalent frequency in the first generation	2.6	2.73	4.15	1.49	3.14	2.83
3. Highest chromosome association	Quadrivalents	Pentavalents	Octavalents	Penta and hexavalents	Quadrivalents	Octavalents
4. Type of change in further generations	a	a	a		a	a+b
5. Crossability with diploids	Incompatible	Compatible	Compatible		Incompatible	Compatible
6. Aneuploid progeny	–	–	Present even in C5 generation	Infrequent	Nil	Present even in C8 generation
7. Reversion to diploidy	–	Present	Frequent	Infrequent	Absent	Small percentage

a = Reduced quadrivalent and increased bivalent frequency; b = Increased quadrivalent frequency.

attributed to increased bivalent frequencies associated with decreased quadrivalent frequencies, i.e., due to gradual diploidization of the autotetraploids. Since this gradual diploidization would require altered pairing relationships at zygotenepachytene, associated with changes in frequency and distribution of chiasmata among the paired chromosomes, an analysis of these aspects is essential to an understanding of the cytogenetic mechanism of improved fertility in autotetraploids. Narasinga Rao (1978) and Arundhati (1980) investigated these aspects in autotetraploids induced by colchicine in an open pollinated line; the open pollinated line was expected to be heterozygous at a large number of loci, including those concerning meiotic behaviour and fertility, and hence should be amenable for selection for fertility. Narasinga Rao (1978) reported that fertility had a genetic basis and it was possible to obtain lines through selection with significantly higher and lower fertility than the base population (C_0 generation) on which selection was practised; further un-selected populations maintained through open pollination did not deviate significantly from the base population in seed fertility. He observed that increased seed fertility in the selected populations was associated with increased chiasma frequency, increased quadrivalent frequency and regular distribution of chromosomes at anaphase I. Similarly, percentage of seed set showed significant negative regression on frequencies of univalents, and trivalents and on the proportions of anaphase I PMCs with laggards. Arundhati (1980) practised further selection on these highly fertile lines of Narasinga Rao, as well as in two other tetraploid lines. In all these lines (including the highly fertile lines of Narasinga Rao as base populations) she found significant response to selection for both high and low fertility and significant associated changes in meiotic features. In all the samples she confirmed the regressions reported by Narasinga Rao (1978) between seed fertility and meiotic features. Arundhati (1980) investigated, apart from the meiotic features in relation to fertility, the relationship of chromosome associations to chiasma frequency. The regression of quadrivalents on chiasma frequency was positive and significant based on cell population means, showing that pearl millet chromosomes frequently exchange partners. In spite of positive association between quadrivalents and chiasma frequency, genotypic interference causing redistribution of chiasmata in favour of bivalent type of pairing at the expense of quadrivalents was also observed. Arundhati (1980) reported that in most plants, the quadrivalent frequencies did not show significant deviation from binomial distribution, demonstrating that the quadrivalent formation between the seven sets of four chromosomes was random. However, when the randomness of associations involving all the four chromosomes of each homologous set was tested an element of non-randomness was observed in chromosome pairing pattern in a few samples.

Aneuploid plants in the progenies of autotetraploids contribute to the proportion of sterile plants in a population. However, aneuploid progeny do not occur always (Table 1) and Arundhati (1980) observed that

aneuploid gametes are transmitted probably through the female side only.

In contrast to earlier reports, Narasinga Rao (1978) observed that the tetraploids were more robust, with larger and darker green leaves, and thicker ear heads than the diploids, i.e. with a number of desirable characters for which a plant breeder looks. However, Arundhati (1980) did not observe the accumulation of such desirable morphological characters in some of the highly fertile lines. This suggests that genes controlling morphological characters segregate independently of those controlling fertility. Further, the presence of a vigorous plant type with gigas characters in some highly fertile lines indicates that polyploidy per se is not limiting to plant vigour as suggested by Minocha et al. (1972).

7 Aneuploids

7.1 Primary Trisomics

All the seven primary trisomics of pearl millet have been described by Gill et al. (1970a, from triploids) and Manga (1972, 1976 from a triploid and desynaptics). The trisomics for chromosomes 1 to 6 were reported to be morphologically distinguishable from each other and also from the diploid, but the trisomic 7 seems to be indistinguishable from the diploid (Table 2). All the trisomics were generally weaker than the diploids.

Virmani and Gill (1971) reported variation in the frequency of trivalent formation for the different trisomics, which seems to be related to chromosome length (Table 2). However, Manga (1976) did not find a correlation between trivalent frequency and chromosome length. The low trivalent frequency observed in the Dwarf trisomic, which involves the longest chromosome of the complement was attributed to the low chiasma frequency. She reported the highest chiasma frequency of 13.0 per PMC for the Purple trisomic, which was significantly higher than that for the diploid sib (12.45 per PMC). She concluded that the effects of individual chromosomes on chiasma frequency were different as can be expected when chiasma frequency is under genetic control.

The transmission frequencies of the trisomic chromosomes were reported to be poor (Table 2). Minocha et al. (1976) observed that in the selfed progenies of the trisomics and in the crosses trisomic × diploid and diploid × trisomic, trisomics constituted 3.4, 7.7, and 1.3 per cent respectively, while Manga (1972) also recorded that the highest frequency did not exceed 14 per cent for any chromosome either through selfing or crossings. Minocha et al. (loc. cit.) attributed the low transmission frequency to the subnormal development of trisomic seeds, their poor and delayed germination and reduced vigour. Selecting small seeds from the different trisomics and growing them separately improved the recovery of the trisomics.

Table 2. Phenotypes and cytogenetic characteristics of the seven primary trisomics of pearl millet

		Trisomic 1	Trisomic 2	Trisomic 3	Trisomic 4	Trisomic 5	Trisomic 6	Trisomic 7	
1. Phenotype	a)	Tiny	Dark green	Lax	Slender	Spindle	Broad	Pseudo-normal	Gill et al. 1970a
	b)	Dwarf	Bush	Semi-dwarf	Slender	Purple	Robust	Pseudo-normal	Manga 1976
2. Trivalent frequency % (diakinesis)	a)	84.0	66.0	43.0	48.0	44.0	35.0	24.0	Virmani and Gill 1971
	b)	50.5	64.5	70.5	60.0	77.5	70.0	25.5	Manga 1976
3. Chiasma frequency. Mean per cell at diakinesis		11.14	12.34	12.75	12.55	13.0	12.5	12.82	Manga 1976
4. Transmission frequency (per cent)	a)	7.5	10.0	6.8	1.7	8.4	2.3	15.8	Minocha et al. 1976
Through eggs	b)	13.64	5.0	10.0	5.0	10.0	5.0	5.0	Manga 1972
Through pollen	a)	0.0	3.7	0.0	5.0	2.0	0.0	–	Minocha et al. 1976
	b)	5.0	4.0	6.65	–	8.0	–	–	Manga 1972
Through selfing	a)	8.3	4.4	3.7	3.9	2.3	2.1	6.1	Minocha et al. 1976
	b)	8.75	12.5	10.0	10.0	14.0	5.0	6.0	Manga 1972

7.2 *Monosomics*

A case of monosomic condition was reported by Jauhar (1970a) but this plant was very weak and completely sterile. Pantulu et al. (1976) reported a case of monotelodisomic condition where the plant was deficient for one arm of a chromosome i.e. a monosomic for one arm. Koduru et al. (1980) investigated the cytology of a plant with $2n=13$ chromosomes which turned out to be a translocation monosomic i.e. a translocation heterozygote with a monosomic complement. In this case the nucleolar chromosome was involved.

7.3 *Other Aneuploids*

In addition to the primary trisomics, double trisomics ($2n+1+1$) (Gill et al. 1970b; Gill and Virmani 1971a; Manga 1972; Pantulu and Rao 1977c) triple trisomics, tertiary trisomics (Gill and Virmani 1971b; Minocha et al. 1974; Tyagi 1975c; Pantulu and Rao 1977b; Venkateswarlu and Mani 1978; Murty et al. 1979) and interchange trisomics (Laxmi et al. 1975a; Minocha and Brar 1976; Narasinga Rao and Narayana Rao 1977; Manga 1977) were also reported.

Pantulu and Manga (1972a) reported the cytogenetics of two plants with $2n=16$, originating in the X_2 generation of seeds irradiated with gamma rays. The extra chromosomes with small deficiencies in their short arms were the shortest in the complement. They paired among themselves but did not pair with other chromosomes. Further, they produced persistent nucleoli at metaphase I, cytomixis, variation in the chiasma frequency and differential condensation in other chromosomes. Thus their cytogenetic effects were similar to those of four or five standard B-chromosomes on the A-chromosome complement. Mani (1973) reported the occurrence of 2–4 centric fragments in the progeny of a triploid plant, which produced no apparent morphological deviations.

8 Interchanges

In recent years chromosome interchanges have received considerable attention in the cytogenetic investigations of pearl millet.

8.1 *Morphological Effects*

Though several spontaneous and induced chromosomal interchanges were reported in pearl millet, in only one case Koduru (1978) observed that a spontaneous interchange was accompanied by a conspicuous difference in morphology from the standard homozygote. The interchange homozygote was a semidwarf with dark green, erect and narrow leaves and early maturity; all these characters were inherited as a group of recessive phenotypes.

8.2 *Cytological Behaviour and Fertility*

Koduru (1978) studied the cytogenetics of two spontaneous interchanges, T3–6 (the semi-dwarf phenotype) and T1–3; the chromosomes involved in the two interchanges and the location of the break points were identified by pachytene analysis. By crossing the two interchange homozygotes to different inbred lines with standard karyotype, he studied the cytogenetic behaviour of the two interchanges in different genetic backgrounds.

At diakinesis both the interchanges formed open ring of four chromosomes in more than 90% of the PMCs in all genetic backgrounds. Formation of a chain of four chromosomes would indicate the failure of chiasma in one of the four arms of the cross-shaped configuration formed at pachytene. Depending on the shape of the chain multiple at diakinesis, Koduru (1979) noted that failure of a chiasma in the four arms was not at random, as it was less frequent in the arm adjoining the homologous centromeres of chromosomes 3 and 3^6 in T3–6 and those of chromosomes 1 and 1^3 in T1–3. The reasons for this non-random failure of chiasma were not deduced. Koduru (1979) recognised five orientation types of the ring and chain multiples at metaphase I: alternate 1, and alternate 2, in addition to adjacent 1, adjacent 2 and indifferent. The relative frequencies of various orientation types were influenced by a change in the genetic background. For these interchanges, homologous centromeres do not seem to play a predominant role in the co-orientation of the interchange multiple. Further the non-homologous co-orientation types were subjected to genetic regulation more than the homologous co-orientation.

Powell and Burton (1969) reported that pearl millet was unlike corn or *Sorghum* (where a single heterozygous interchange reduces pollen fertility to 50%), and was more like tomato and barley where a single interchange results in 67 to 77% pollen fertility, and two interchanges are necessary to reduce fertility to 50%. However, other investigators reported widely variable pollen sterility (42–71%) for the different interchanges (Tyagi and Singh 1975; Sidhu et al. 1977). Koduru (1979) demonstrated that the sterility for the same interchange can vary depending on the genetic background of the plant. Further, pollen and ovule fertility for an interchange were closely correlated with the percentage of alternate co-orientation of the interchange multiple at metaphase I which was subjected to genetic control (Koduru 1979).

8.3 *Breeding Behaviour*

In the selfed progenies of plants heterozygous for a chromosomal interchange, standard homozygotes,

heterozygotes and interchange homozygotes are expected in the proportion of 1 : 2 : 1, assuming normal viability of gametes carrying the interchanged chromosomes and normal viability of zygotes of all three genotypes. This expectation was realised for 51 induced interchanges (Tyagi 1975 b; Sidhu et al. 1977) and for one spontaneous interchange T (3–6) (Koduru 1978). However, the inheritance of two interchanges (T–9, an interchange involving chromosomes 1 and 2, and T–40 involving chromosomes 1 and 5) studied by Tyagi (1975 b) deviated from the expectation and the causes for deviation were not explained. Sidhu et al. (1977) found a higher transmission of the interchanged chromosomes through ovules than through the pollen.

8.4 Tester Stocks

Tyagi and Singh (1975) and Tyagi (1975 b) produced several interchanges by gamma ray irradiation in the inbred I 55 and assembled a tester set of five translocation stocks consisting of T1–5, T1–7, T2–4, T3–4, and T3–7. Using this tester set, in any new interchange all chromosomes but the sixth can be identified and chromosome 6 can also be identified by the process of elimination. Tyagi (1975 b) presented the detailed data. Minocha et al. (1979) also established translocation tester sets representing breaks in all the seven chromosomes.

Tyagi (1976 a) demonstrated the use of the tester set for the identification of the chromosomes involved in new interchanges. He also used the tester set to identify the extra chromosome in primary trisomics (Tyagi, 1976 c). In a trisomic plant of the F_1 hybrid between a primary trisomic and an interchange tester stock, an association of five chromosomes plus five bivalents would indicate that the extra chromosome in the primary trisomic is homologous to one of the two translocated chromosomes in the tester stock. In contrast, if the extra chromosome of the trisomic is not homologous to either of the two translocated chromosomes in the tester, the 15 chromosomes would pair as an association of 4, one trivalent and four bivalents.

8.5 Complex Interchange Stock

Several attempts to synthesize a stock of pearl millet with all the seven chromosomes of the haploid set forming a single multiple interchange complex (complete interchange stock) have been reported (Brar, Minocha and Gill 1973; Jauhar 1972, 1974; Tyagi and Singh 1974; Tyagi 1976 b). The principal use of such a stock would be for practising the *"Oenothera"* method of gamete selection (Burnham 1946) for isolating inbred lines which could be used for breeding heterotic hybrids (Tyagi 1976 b). Small chromosome number, large size of the chromosomes, median or submedianly placed centromeres in most of the chromosomes and complete terminalization of chiasmata by diakinesis are cytological characters of bajra conducive to the synthesis of such a complete interchange stock. Tyagi and Singh (1974) and Tyagi (1976 b) have succeeded in synthesizing such a complete interchange stock, a homozygous line which on crossing to standard normal plants produced hybrids with a ring of 14 chromosomes, by adopting the method of recurrent intercrossing and irradiation starting with lines homozygous for single but different interchanges. However, the interchange heterozygotes with a ring of 14 chromosomes were almost totally sterile making it impractical to adopt the *"Oenothera"* method of gamete selection and production of useful inbred lines. As pointed out by Tyagi (1976 b) the synthesis of such a stock may not be completely purposeless, because the totally sterile interchange hybrids would still be useful for evolving heterotic hybrids for forage, where seedlessness is useful, and also for testing genetically controlled apomixis. Moreover, as demonstrated by Koduru (1979) alternate orientation of interchange multiples at metaphase I leading to increased fertility is under genetic control, which suggests the possibility of improving the fertility of the complex interchange stocks by genetic manipulation.

In another inbred line 'BIL 4', interchange heterozygotes were initially produced by gamma irradiation and plants homozygous for several interchanges were developed by intercrossing the initial interchange lines. However, this procedure resulted in stocks involving up to ten chromosomes only in interchanges, and only after recurrent irradiation with gamma rays were plants with ring of 14 chromosomes obtained. Since these heterozygotes were highly sterile Brar et al. (1973) could not obtain a complete interchange stock in homozygous condition.

Jauhar (1974) adopted the method of recurrent irradiation of seeds with gamma rays. In each generation interchange heterozygotes were identified and their seeds were used for the next round of gamma irradiation. Even after seven doses of recurrent irradiation interchanges involving only 12 of the 14 chromosomes were obtained, and further cycles of irradiation and intercrossing did not produce a ring of 14, which was attributed to the more vigorous operation of somatic and gametic sieves when more chromosomes were involved in interchanges. Laxmi et al. (1975 a) reported the occurrence of a ring of eight chromosomes in one plant following mutagen treatment. They found that gamma rays were more efficient than EMS in producing chromosomal interchanges and the inbreds differed considerably in their response to mutagens. The frequency of translocations increased linearly with an increase in the dose of gamma rays up to 20 kR and in square of the dose relationship above 20 kR, while it decreased with increasing dose of EMS. Lal and Srinivasachar (1979 a) concluded that alternate use of Ethyleneimine (EI) and gamma rays offered better possibilities of obtaining interchange heterozygotes involving more, if not all, chromosomes in a

ring than two successive treatments with gamma rays alone. They also reported that different varieties were differently responsive to all the mutagens (Gamma rays, EMS and EI) investigated by them. Varietal difference in sensitivity to gamma ray treatments was reported as well by Hanna and Young (1974), who used pollen instead of dry seeds as used by other workers. Their study revealed that 3 kR was the most effective dose for the production of chromosomal aberrations. Tyagi (1978) observed that the translocation break points were disproportionately distributed in relation to chromosome length. In general the longer chromosomes tended to have more than and the shorter chromosomes less than the number of breaks expected in them.

8.6 A-B Chromosome Translocations

Pushpa (1980) reported a case of translocation of a short segment of the nucleolar organizer short arm of chromosome 7 to the heterochromatic short arm of a Standard B-chromosome. Thus it was a case of simple translocation, occurring in a sample of seeds treated with 0.3% EMS.

9 Genetic Control of Mitosis and Meiosis

The genetic control of mitosis and meiosis in pearl millet is poorly understood inspite of the fact that several nuclear abnormalities have been described. An experimental approach to the study of mitosis and meiosis has started only recently.

9.1 Duration of the Mitotic Cycle

Duration of the mitotic cycle in bajra was estimated to be 23.0 h in the primary root meristems from germinating seeds at 30±2 °C by colchicine shock method (Krishna Rao et al. 1979).

The duration of the mitotic cycle was also estimated in the young embryo and endosperm from the field grown material in two inbred lines Vg 212 and PDP of bajra (Krishna Rao and Aswanikumari, unpublished). The first mitotic division in the primary endosperm nucleus was completed in less than 6.0 h after pollination, while the first division in the zygote was completed in less than 24 h after pollination. In the first 48.0 h after pollination the endosperm undergoes about nine divisions and during this phase of free nuclear endosperm development the mean cycle time was 6.0 h. However, the mean cycle time increased to about 17±1 h in Vg 212 and to 10.0–11.0 h in PDP at 72 h after pollination at which time the endosperm becomes completely cellular. The mean cycle time in the embryo decreased to 8.0–9.5 h up to the sixth cycle, which occurred about 72.0 h after pollination, and again increased to about 18.0–20.0 h after cellularization in the endosperm.

9.2 Numerical Mosaicism

Chromosome numerical mosaicism, i.e., cell to cell variation in the number of chromosomes, was reported in the PMCs by Sharma and De (1956) and by Patil and Vohra (1962). The genetic basis, if any, of these two cases was not reported.

A case of genetically controlled chromosome mosaicism was studied in detail by Pantulu and Rao (1977d). Chromosome number varied from 24 to 37 in the root tip cells and from 28 to 37 in the PMCs. Earlier, Gildenhuys and Brix (1964) recorded mosaicism in the amphiploid, *P. typhoides* × *P. purpureum* and concluded that it was controlled by recessive genes confined to *P. purpureum*. Pantulu and Rao (1977d), on the other hand, concluded that the genes controlling mosaicism were present in pearl millet also. Further, the mosaicism in pearl millet seemed to result from certain gene combinations and was not always associated with higher gene dosage and higher polyploidy as suggested by Gildenhuys and Brix (1964).

9.3 Multiploid Sporocytes

Pantulu and Manga (1971) described a recessive mutant condition specifically expressed during the premeiotic mitoses in the anthers. Designated as *"multiploid sporocytes"* (*mu*) the mutation suppressed wall formation during mitoses in the sporogenous cells and resulted in multinucleate plasmodial masses. The presence of plasmodia with several nuclei and up to 256 pairs of chromosomes indicates that the gene expresses several cell generations before the onset of meiosis. Once initiated, suppression of wall formation seems to persist, because formation of four normal uninucleate microspores at the completion of meiosis occurred only in the PMCs with diploid nuclei, but not in the plasmodia.

In contrast to this *mu* mutant, a spontaneously occurring male sterile mutant (ms_2), also producing plasmodial sporocytes, described by Krishna Rao and Koduru (1978a) is strictly a meiotic mutant. Homozygosity for ms_2 produced plasmodial tapetum, delayed and asynchronous meiotic development, desynapsis and blockage of meiosis also. Plasmodia resulted from the fusion of uninucleate PMCs initiated at pachytene; as cell fusion continued, larger plasmodia with greater number of nuclei were formed with increasing maturity of the anther.

9.4 Synaptic Variants

One of the frequently reported phenomena is the occurrence of univalents in meiosis, either spontaneously

or under a wide variety of experimental conditions. The univalent formation is mostly attributed to desynapsis and its study is largely confined to a description of the phenomenon and the behaviour of univalents (Patil and Vohra 1962; Jauhar 1969a; Singh et al. 1977a; Lakshmi and Yakob 1979).

Dehsi et al. (1973) recorded spontaneous occurrence of desynapsis in the stock BG-32. Later Minocha et al. (1975) reported its inheritance as a monogenic recessive trait. Pantulu and Subba Rao (1976) obtained a desynaptic mutant after colchicine treatment which was also a monogenic recessive. In this mutant 14 univalents were present in a large number of PMCs and the mean chiasma frequency was 0.68 per cell.

Subba Rao (1980b) found that the colchicine mutant was allelic to another desynaptic mutant of spontaneous origin. Considerable variation was observed in the number of univalents per PMC at diakinesis and metaphase I and it was suggested that the variation might be due to the presence of modifying genes, since the partial desynaptics on selfing gave rise to complete desynaptics.

In the frequency of bivalent formation, there were no significant differences between the basal, middle and upper segments of an anther, or between the anthers of a spikelet or between the spikelets of a plant. However, there were significant differences in frequencies of bivalents between plants and between seasons.

The bivalent frequency significantly deviated from binomial distribution indicating non-random formation of bivalents. The deviation from binomial distribution in a large number of plants fits Model 1 of Srinath and Sinha (1968) though a few plants fit Model 2. It was argued that the cytological data and the model fitting revealed the existence of intra-cellular differences which result in the differential behaviour of chromosomes within PMCs. However, the possibility of the existence of inter-cellular differences was not ruled out.

Krishna Rao and Koduru (unpublished) and Lakshmi et al. (1979) investigated the cytogenetics of spontaneous desynaptics in the inbred line IP 1475. In this line plants showing partial or complete desynapsis or asynapsis, were found to segregate in some families after several generations of inbreeding. In some of the abnormal plants chromosome fragmentation was also present. Though the genetic basis of these meiotic abnormalities was not clearly understood, Lakshmi et al. (1979) reported one family in which desynapsis accompanied by chromosome fragmentation resulted from the action of duplicate recessive factors.

Koduru (1980) reported that the meiotic behaviour of univalents in the desynaptic plants was different from that in the asynaptic plant. In desynaptic plants univalents were found to divide at anaphase II, while in the asynaptic plant in 68.6% of the PMCs all the 14 univalents in each PMC were found to divide at anaphase I. Therefore, it appears that there is a correlation between the lack of chromosome pairing at pachytene (asynapsis) and equational division of univalents at first anaphase.

Usually desynaptic and asynaptic plants exhibit other abnormalities. Patil and Vohra (1962) recorded in the desynaptic plant poor spindle development, non-orientation of some univalents, clumping of the chromosomes on the equatorial plates, and chromosome mosaicism. Krishna Rao and Koduru (1978b) observed chromosome breakage, exaggeration and stretching of the centromere, chromosome stickiness and neocentric activity. In this plant, distribution of the sites of breakage was non-random as it was confined to the centromeres and chromosome ends. Moreover, breakage in the centromere was twice as frequent as that in the end segments. Furthermore, nucleolar chromosomes were involved less frequently than others in breakage and stickiness.

Desynapsis was also reported in the autotetraploid genotypes (Koduru and Krishna Rao 1978; Subba Rao 1978, Narasinga Rao 1978), which was mainly expressed as a drastic reduction in the frequency of chiasmata and multivalent formation and an increase in the frequency of univalents.

Recently there have been some attempts to understand the factors that affect desynapsis. Dehsi et al. (1975) found increased chiasma frequency and thus decreased desynapsis, with an increase in the appliction of phosphate and potassium to the soil. Lakshmi et al. (1979) estimated the quantities of phosphate and potassium in desynaptic and normal plants to investigate whether the desynaptic mutants were deficient for those ions in their plant body at the time of meiosis, and therefore, whether the positive response in chiasma frequency was due to partial or complete compensation of the deficiency due to the increased availability of these substances in the soil. However, they concluded that the desynaptic plants were not deficient either in phosphate or in potassium in the flag leaf at the time of meiosis of the PMCs.

9.5 Induction of Meiotic Abnormalities

Srinivasachar and Mohandas (1971) investigated the effect of hydroxylamine (HA), ethylmethane sulphonate (EMS) and gamma rays on the meiotic chromosomes of pearl millet. They reported that HA treatment following 20 kR of gamma rays reduced the frequency of associations of four chromosomes presumably by inhibiting rejoining and restitution of chromosomal breaks while HA following 30 kR gamma rays increased the frequency of quadrivalents and hence presumably acted as a promoter of rejoining and restitution of chromosome breaks. EMS following 20 kR of gamma rays, and HA following 0.6% EMS also reduced quadrivalent frequencies. Laxmi et al. (1975b) reported, in both inbred lines and commercial hybrids after treatment with gamma rays and/or EMS, the occurrence of chromatin bridges, fragments, micronuclei, laggards and unequal separation of chromosomes; the last mentioned two abnormalities were the most frequent types.

They found that gamma rays were more effective than EMS or the combination treatments in inducing cytological anomalies. Lal (1978) also described a number of meiotic abnormalities, including the formation of pseudo-Iso-chromosome rings in the M 1 plants following mutagen treatments of dry seeds. The efficiency of mutagens in inducing abnormalities at anaphase I followed the order for variety 'BIL 3E', gamma rays > DES > MH > EI; and for the variety 'Tift-23B', MH > gamma rays = DES > EI.

Reduced chiasma frequency was observed by Lal and Srinivasachar (1979b) in the M1 plants raised from the seeds treated with gamma rays, DES, EI and MH as compared to their respective controls.

9.6 Other Mutants

A monogenically inherited recessive mutant interfering with post-meiotic cell development was also reported. In the spontaneous male sterile mutant in Vg 272 described by Krishna Rao and Koduru (1978c), pollen grains degenerate before the first mitosis.

9.7 The Effect of Inbreeding on the Endophenotypic Characters

A factor that appears to have largely inspired studies of chromosomal behaviour in relation to inbreeding is the early recognition of "chromosomal phenotype" (differences in morphology and behaviour of chromosomes), which can be subjected to the same kind of analysis as the external phenotype. The endophenotype is also under the control of the genotype and, consequently, its various aspects are subject to selection. Chromosome evolution is achieved through natural selection acting upon the heritable variation affecting their form and function, and in any species the efficiency of the chromosome mechanism will have been improved by selection acting under the operating breeding system. The problem is how a forced alteration in the breeding system will affect the chromosomes; pearl millet is well suited for such a study.

Harinarayana and Murty (1971) observed a consistent increase in mean chiasma frequency per cell in inbreds as compared to the outbred populations; the increase was parallel with the degree of inbreeding. They considered this as a buffering mechanism against the changes (restriction) in recombination that would result from forced inbreeding in a natural outbreeder. However, the observations of Pantulu and Manga (1972b) and Manga and Pantulu (1974) were different. They found that the inbred lines had mean chiasma frequencies significantly lower than those in the open pollinated population, and an increase in the variation in mean chiasma frequency. With increasing inbreeding there was a decrease in the level of efficiency of chromosome behaviour during meiosis in PMCs. Some inbreds were less stable than the others, and they differed genetically in the control of these characters.

The influence of environment on chiasma frequencies of the inbred lines was significant. During the stress-season, there was a significant decrease in the mean chiasma frequencies and an increase in the variation of mean chiasma frequencies. When variations were considered as the measure of stability, the inbred lines differed in their relative stability. It was concluded that as in rye and maize, the inbreeding depression might depend upon the segregation of particular homozygous gene combinations rather than on some specific demerits of homozygotes.

When the inbred lines were crossed all the F_1s attained a level of chiasma frequency and meiotic chromosome behaviour characteristic of that of the natural population, and mean chiasma frequencies of the F_1s were higher than those of their parents, thus exhibiting heterosis for this character. Some of the F_1s showed chiasma frequencies even higher than those in the natural population. The variation in mean chiasma frequency in the F_1s was also smaller than that in the inbred lines, reflecting their greater stability in development in both stress and nonstress seasons. Although this kind of variation was initiated by environmental fluctuations, the amount of variation exhibited depended on the particular genotype. They found that the heterosis for chiasma frequency resulted from average overdominance which was, at least partly, due to non-allelic gene action. Results largely similar to these, particularly on chiasma frequencies, were reported by

Table 3. Chromosome locations of genes in pearl millet

Phenotype	Gene symbol	Chromosome	Reference
Hairy leaf	*hl*	1	b
Purple glume	pg_1, pg_2	1 and 6	a, b, c
Bristled ear	*Br*	2	a, b, c
Yellow foliage striping	*yst*	2	a, b, c
Purple pigmented foliage	Pb_1, Pb_2	2 and 4	b
Purple pigmentation of plant parts	–	2	c
Purple pigmentation of plant	–	4	a
Hairy node	–	4	c
Branched ear base	*Beb*	5	b
Purple node	Pn_1	5	a, b, c
Branched ear tip	*Bet*	6	a, b, c

a = Minocha 1978; b = Minocha and Sidhu 1979; c = Minocha et al. 1978

Scrivastava and Balyan (1977). Their results also suggest a positive association between chiasma frequency and grain yield heterosis.

10 Cytogenetic Maps

Minocha et al. (1978) listed four linkage groups in pearl millet. Bristling with dwarfness (D-57), ear-tip branching, purple glume colour and yellow foliage striping; (2) purple pigmentation of plant parts with naked ear-tip, and yellow foliage striping; (3) hairy node with purple glume colour and (4) yellow leaftip with hairy node, hairy leaf and purple node. Some of the genes have been referred to their respective chromosomes (Table 3).

11 Interspecific Hybrids and Genome Relationships

Though the genus *Pennisetum* is a large one the only two species so far known with a basic number n = 7 are *P. typhoides* (= *P. americanum*) and *P. purpureum*, and morphological similarities are more pronounced between these two species which are also closely related. The two species can easily be crossed even though the hybrid is sterile; occasionally spontaneous doubling of chromosomes occurs (Jauhar 1969 b). However, hybridization was also accomplished between groups differing in basic numbers. For example Gildenhuys and Brix (1961) obtained hybrids between *P. typhoides* × *P. dubium* (2n = 66). Interestingly, only 14-chromosome gametes were received from *P. dubium*. Other successful crosses are between pearl millet and *P. squamulatum* and *P. orientale* (Cf. Burton and Powell 1968; Jauhar 1973), *P. setaceum* (Hanna 1979) and *Cenchrus ciliaris* (Read and Bashaw 1974). Recently a trispecific hybrid *P. squamulatum* × (*P. typhoides* × *P. purpureum*) amphidiploid was obtained and the pairing of chromosomes in meiosis revealed the existence of homology among the chromosomes of the parental species (Sree Rangasamy et al. 1971).

The genome relationships between *P. typhoides* and *P. purpureum* have been described by Krishnaswamy and Raman (1956). Pantulu (1967), Jauhar (1968) and Sethi et al. (1970) studied interspecific hybrids between *P. typhoides* × *P. purpureum*. Here chromosome homologies could be studied with advantage as the chromosomes of the variety of *P. purpureum* employed by Pantulu (1967) have markers like terminal knobs in seven out of the haploid set of 14-chromosomes. From this study Pantulu confirmed the assumption of Krishnaswamy and Raman that *P. purpureum* has two genomes, A and B, and this A genome is homologous with the genome of *P. typhoides*. Chromosomes 1 to 5 of *P. typhoides* are homologous with chromosomes 1 to 5 of *P. purpureum* respectively; chromosomes 6 and 7 of *P. typhoides* are homologous with 8 and 14 of *P. purpureum* respectively. Jauhar (1968) found up to nine bivalents at metaphase I in the hybrid of which up to only five bivalents were heteromorphic i.e., formed by the chromosome pairs belonging to genomes A and A′. Based on this he concluded that autosyndetic pairing of chromosomes occurred within the *P. typhoides* complement (A genome) and also within the A′ genome of *P. purpureum*. The extra bivalents observed were the result of intra-haploid pairing to a maximum of two bivalents within each of the three genomes A, A′ and B of the hybrid.

Sethi et al. (1970) on the other hand reported the modal chromosome configuration as $7_{II}+7_{I}$ supporting the view that *P. purpureum* is an allopolyploid and carries seven *P. typhoides* chromosomes. The occurrence of more than seven bivalents and an occasional trivalent were considered to be the result of allosyndetic pairing and/or chromosomal rearrangements. They also stated that there were indications of certain chromosomal aberrations in *P. purpureum*.

Sreeramulu (1971) studied the cytology of the progenies of an amphiploid of *P. typhoides* × *P. purpureum* (2n = 42) and reported more frequent formation of 21_{II} at diakinesis, supporting the conclusion of Krishnaswamy and Raman (1956). Hanna (1979) observed that the F_1 hybrid of the cross *P. americanum* (2n = 14) and *P. setaceum* (2n = 36) had 25 chromosomes and was male sterile. At metaphase I a few associations between the chromosomes of the two species were present. Somatic elimination of one or two *P. setaceum* chromosomes made it possible to establish clones with different chromosome constitutions and offers the possibility of transferring *P. setaceum* germ plasm to pearl millet, bypassing the sexual process.

Brunken (1977) found that the F_1 hybrids pearl millet × *P. fallax* (2n = 14), and *P. violaceum* (2n = 14) × pearl millet, were morphologically intermediate and highly fertile. The hybrids were also robust and exhibited shattering habit at maturity. The hybrids involving *P. fallax* corresponded to *P. dalzielli* (2n = 14), and those involving *P. violaceum* corresponded to *P. stenostachyum* (2n = 14), two more wild species. These results demonstrate that no genetic isolation exists between pearl millet and its wild progenitors. On a strictly biological basis, therefore, it was not possible to separate these two groups of plants at the specific level (Brunken, 1977).

12 Basic Chromosome Number

Jauhar (1970 b) concluded that the chromosome number of pearl millet, n = 7, was derived from x = 5, based

on his observations of (i) the formation of a maximum of two bivalents per cell, some with two chiasmata each, in the haploid plants, (ii) the significant restriction of intragenomal chromosome pairing in the hybrid *P. typhoides* × *P. purpureum* to two bivalents and (iii) the occurrence of higher association of up to eight chromosomes in the autotetraploid pearl millet. However, Manga and Pantulu (1971) did not observe any chiasmate bivalents in haploid plants. The bivalents observed by Jauhar (loc. cit.) might be the result of translocation heterozygosity present in the diploid progenitor. Moreover, Manga and Pantulu pointed out that as concluded by Levan (1942) for rye, derivation of n = 7 from x = 5 involves tri- or tetrasomic condition which must acquire extremely poor vitality, and immense difficulties must be met before the new form may obtain a balance with its higher chromosome number. It is the experience of pearl millet cytogeneticists that the trisomics are comparatively weak and the transmission frequency of the extra chromosome is very low.

Concerning the intra-genomal pairing of pearl millet chromosomes in the hybrid *P. typhoides* × *P. purpureum,* the observations of Pantulu (1967), Sethi et al. (1970) and Sree Ramulu (1971) do not support such a concept. Pantulu (1967) in particular could differentiate at pachytene the knobbed chromosomes of *P. purpureum* from the knob-less chromosomes of *P. typhoides,* and concluded that pairing was between the chromosomes of *P. typhoides* and their homologues in the A genome of *P. purpureum.* Hanna (1979) also did not report any intragenome pairing of pearl millet chromosomes in the hybrid *P. americanum* × *P. setaceum.*

Concerning the higher than quadrivalent associations in the autotetraploid, Narasinga Rao (1978) and Arundhati (1980) showed that such pairing can be a consequence of translocation heterozygosity, as some of the revertant diploids obtained from these tetraploids were translocation heterozygotes.

Another point generally cited to support five as the basic chromosome number for this genus is the genome of *P. ramosum* (Jauhar 1970b; Minocha et al. 1972), which has n = 5 and the chromosomes are the largest in the genus. Probably *P. ramosum* is not a primitive species as judged by its limited distribution and apomictic reproduction (Narayan 1954). Further, Avdulov (1931) concluded that phylogenetic trends within the family have been from higher basic number and smaller chromosome size to low basic number and larger chromosomes. Bearing in mind that chromosome number n = 9 is uniformly present in the tribe Paniceae (except in the genus *Paspalum* with n = 10 and 12) it is more in keeping with the evidence to trace in *Pennisetum* species with n = 7 a reduction in chromosome number and increase in size than to trace an increase in number from n = 5. In all species of *Pennisetum* with x = 9, chromosomes are small, while in *P. typhoides* and *P. purpureum* with x = 7 the chromosomes are medium sized. In *P. ramosum* (n = 5) are seen the largest chromosomes among the tribe Paniceae, so far.

13 Conclusion

The initiation of a world wide collection of pearl millet germ plasm, its maintenance and evaluation at the International Crop Research Institute for Semi-Arid Tropics (ICRISAT), India, emphasizes the importance that is being paid to this crop plant in recent years. It is hoped that in future pearl millet will receive increased attention from cytogeneticists, not only as a crop plant but also as an organism for basic genetic research that is truly commensurate with its great potentialities as a cereal food for the people of the semiarid tropics.

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