Theoretical and Applied Genetics 42, 69–74 (1972)

Cytology of Inbreds and F_1 Hybrids of Pearl Millet

J. V. PANTULU and **V. MANGA**

Department of Botany, Andhra University, Waltair (India)

Summary. The meiotic behaviour of chromosomes was studied in four inbred lines and their F_1 hybrids of *P. typhoides*. The inbred lines showed a decrease in mean chiasma frequency when compared with the population plants, but differed from one another in their mean chiasma frequencies. Together with the decrease in mean chiasma frequency the inbreds showed variation in mean chiasma frequencies. The inbred lines showed a number of meiotic abnormalities such as extra chromosomes, extra fragments, desynapsis, persistent nucleoli and differential condensation of chromosomes. The F_1 hybrids of these inbreds exhibited heterosis for chiasma frequency. All the F_1's had mean chiasma frequencies higher than the means of the respective participating parents. The F_1's, however, differed in the degree of heterosis exhibited. In the F_1 hybrids, the variation in mean chiasma frequency, both between plants and between PMC's within plants, was significantly lower than that of the inbred lines. The effect of environment was studied in the inbred lines and their F_1 hybrids. The mean chiasma frequencies of the inbred lines were significantly lower, and the variation in mean chiasma frequencies was greater, in the stress season. The mean chiasma frequencies of F_1's did not show any significant differences between the two seasons. The F_1's exhibited less variation in mean chiasma frequency than the inbred lines, showing that F_1's were developmentally more stable. The F_1's did not show any meiotic abnormalities in either season.

Introduction

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 constitute different aspects of the chromosomal phenotype, which can be subjected to the same kind of analysis as the more easily observable components of the external phenotype. It is important to note that 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 imposed by selection acting under the operative breeding system (Rees, 1955). The problem is how a forced alteration in the breeding system will affect the chromosomes. Much of the pertinent information up to now has been obtained from rye and, to some extent, from maize.

In rye, which is an outbreeding species, Lamm (1936), Müntzing and Akdik (1948), Rees (1955 a–b), Rees and Thompson (1956) and Sybenga (1958) have shown that the behaviour of the chromosomes is less efficient in inbred plants than in the original population. Rees (1955 a, b) demonstrated that, in comparison with outbred populations, all the inbred lines in rye showed a reduction in chiasma frequency and greater variation in mean chiasma frequency. The inbred lines varied from one to another, which would be expected from the segregation of genes controlling chiasma formation. Rees has also shown that, together with decreasing chiasma frequency with inbreeding, an increasing number of structural and other abnormalities of the chromosomes and aberrant types of chromosomal behaviour emerge. These also must be characteristic of particular gene combinations because the abnormalities vary between lines. Rees (1955b, 1961) and Rees and Thompson (1956), in studies of inbred lines and their F_1 combinations in rye, have demonstrated heterosis for chiasma frequency, as would be expected in view of the known effects of inbreeding. They have also demonstrated that this heterosis was controlled in the same way as heterosis for many characters of the external phenotype, depending at least in part on interaction between non-allelic genes.

Pearl millet, *Pennisetum typhoides*, an important crop plant, is very well suited to a study of the effects of inbreeding on the endophenotypic characters. The plant is naturally crossbreeding, the chromosomes are few ($2n = 14$) and fairly large and easy to handle. The present paper deals with the comparative cytology of inbred lines and their F_1 hybrids.

Materials and methods

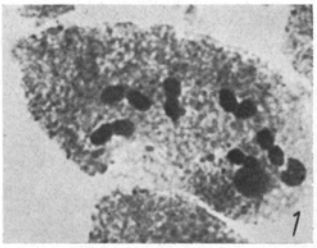
The material used for this study consisted of four inbred populations with $2n = 14$ chromosomes. They were subjected to forced inbreeding by selfing for 6 to 10 generations. Of the four inbred lines, three were local lines selfed for 10, 9 and 7 generations, and the fourth one was a Sudanese line selfed for 6 generations.

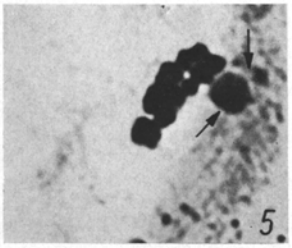
F_1 families were produced by effecting crosses in all combinations among the four inbred lines. The seed from reciprocal crosses was pooled and the progeny plants were scored without any reference to the way in which the cross was effected. The inbreds and their hybrids were grown in the main season (June–October) and second season (January–April).

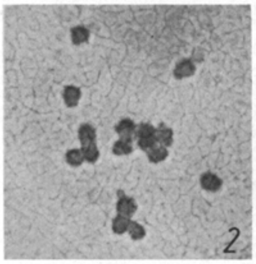
For the study of chiasma frequency at metaphase I, young ear-heads were fixed in 1:3 acetic acid – absolute alcohol mixture. Chiasma frequency was counted from not less than 20 PMC's in each plant. The mean chiasma frequency values, their SD and CV, were used as the measures of comparison. The differences existing between the inbred lines, between plants and within plants, were obtained from the analysis of variance tests. The three local inbred lines were denoted by the letters A, B and C, and the Sudanese inbred line by the letter D.

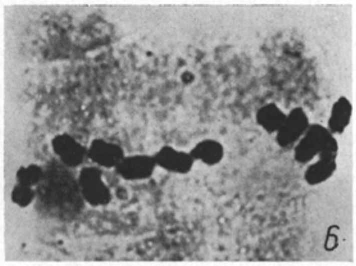
Results

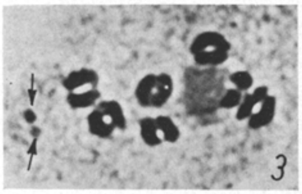
Analysis of inbred lines: Data on the mean chiasma frequency per nucleus at metaphase I for the four inbred lines for the two seasons are presented in Table 1. The first half of the table deals with the data for the main season and the second half with the second season data.

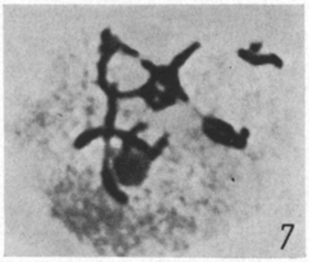


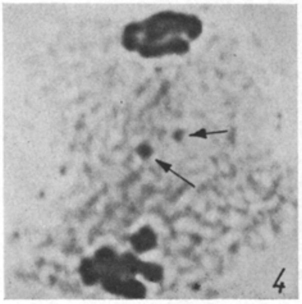












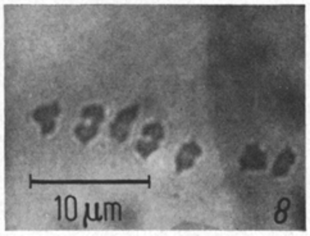


Fig. 1: Diakinesis stage in inbred A showing six rod bivalents and one ring bivalent giving eight chiasmata

Fig. 2: Metaphase I showing trisomic condition ($2n = 14 + 1$); four bivalents and seven univalents

Fig. 3: Diakinesis stage showing seven bivalents and two extra fragments

Fig. 4: Anaphase I showing two fragments lagging

Fig. 5: Metaphase I showing persistent nucleoli of different sizes

Fig. 6: Diakinesis stage showing one bivalent and 12 univalents (Desynapsis)

Fig. 7: Diakinesis showing differentially condensed bivalents

Fig. 8: Hybrid C × D showing seven ring bivalents at metaphase I giving a total of fourteen chiasmata

Table 1. *Mean chiasma frequency, standard deviation and coefficient of variability in the inbreds and F1 hybrids in the main and second season*

	Main season			Second season		
Inbred/ hybrid	Mean chiasma frequency	Standard deviation (SD)	Coefficient of variability (CV)	Mean chiasma frequency	Standard deviation (SD)	Coefficient of variability (CV)
A	9.494	1.5189	16.113	7.56	1.4060	17.9740
B	11.180	1.1009	10.0236	7.67	1.1277	13.4710
C	12.030	0.9089	7.3164	10.49	0.9826	9.3825
D	12.075	0.6330	5.5065	11.875	0.5889	4.9037
A×B	12.630	0.3723	2.9740	12.630	0.3825	2.9838
A×C	13.285	0.3821	3.0490	13.200	0.3469	2.6154
A×D	13.205	0.3247	2.4460	13.280	0.3732	2.7918
B×C	12.740	0.3971	3.1250	12.750	0.4007	3.1539
B×D	12.520	0.4114	3.2430	12.480	0.4117	3.2617
C×D	12.800	0.3788	2.9330	12.800	0.2707	2.1325

The data for the main season showed that the chiasma frequency in all the inbred lines was significantly lower than that in the original population plants, from which these inbreds were developed. The inbred A, selfed for 10 generations, showed the lowest mean chiasma frequency i. e., 9.47 and next, in order, were the inbreds B, C and D with mean chiasma frequencies of 11.18, 12.03 and 12.075, respectively.

In the second season, the chiasma frequency of the inbred lines showed considerable reduction when compared with the main season. Inbred A showed a mean chiasma frequency of 7.56, (Fig. 1) and inbred B, 7.67, compared with 9.47 and 11.17, respectively, in the main season. These two inbred lines exhibited the maximum reduction in chiasma frequency. For C and D the differences in chiasma frequency in the two seasons were comparatively less.

Variation between inbred lines: The analysis of variance test presented in Table 2 shows that the four inbred lines differed from one another in their mean chiasma frequencies, and the differences were significant in the main as well as in the second season, since the calculated '*F*' value exceeded the value from '*F*' tables (F_3, $27 = 2.96$) at the 5% level of significance (Table 2). The inbred lines also differed in the nature and frequency of meiotic abnormalities (Table 6).

Variation within inbred lines between individuals: As well as the decrease in mean chiasma frequency, a greater variation in mean chiasma frequency was observed in all the inbred lines. The mean chiasma frequency was calculated from ten randomly selected plants from each of the inbred lines. The variation between plants within each inbred line was tested by analysis of variance, and the data showed significant variation in all the inbred lines since the observed '*F*' value was greater than the value from '*F*' tables (F_9, 27 = 2.2) at the 5% level of significance (Table 3).

Variation between PMC's in inbred plants: The analysis of variance tests showed significant variation within plants in all the four inbred lines in both the seasons since the calculated '*F*' value exceeded the table value for '*F*' at 5% level (F_{19}, 171 = 1.654).

Of the four inbred lines inbred A was showing greater variation in the main season as well as in the second season. Next in order of variation of mean chiasma frequencies were inbred lines B and C. Inbred D was not showing any significant difference between the two seasons.

Meiotic abnormalities in inbred lines: Together with the decrease in mean chiasma frequency with inbreeding there occurred a number of meiotic abnormalities. These were trisomy, fragments, persistent nucleoli, desynapsis and differential condensation of chromosomes. A larger number of inbred plants showed all the abnormalities listed in the second season than did so in the main season, where only a few plants showed abnormal meiosis (Table 6). A detailed account of these abnormalities is given below.

Trisomy: This phenomenon was observed in one plant out of a population of 25 plants of the inbred A in the second season. The presence of the extra chromosome was observed in only 5% of the PMC's at diakinesis and metaphase I. The extra chromosome formed a trivalent in 2% of the cells and in others it was left out as a univalent (Fig. 2).

Fragments: Two extra fragments were observed in one plant out of a population of 25 plants of inbred A in the second season. The fragments were observed in 10% of the PMC's and they measured less than half the length of the shortest A-chromosome of the complement (Fig. 3). The fragments were moving to the poles without dividing at anaphase I. In 2% of the cells these fragments were lagging at telophase I (Fig. 4).

Table 2. *Analysis of variance of PMC chiasma frequency between inbred lines and between plants of inbred lines in two seasons*

Source of variation	DF	SS	MS	'F' Statistic
Inbreds in main Season				
Between Inbreds	3	39.65	13.216	57.28*
Between Plants	9	14.65	1.627	7.649*
Error (within lines and within Plants)	27	6.23	0.2308	–
Total	39	60.53	–	–
Inbreds in second Season				
Between inbreds	3	136.68	45.56	462.0*
Between Plants	9	11.05	1.227	12.46*
Error (within inbreds and within Plants)	27	2.661	0.0986	–
Total	39	150.391	–	–

* Significant at 5% level.

In those cases where a fragment divided during the first division, it was not observed to divide during the second division but moved to one of the poles, resulting in half the microspores having one fragment and the other half no fragments. In 18% of the cells, a single fragment was observed in one of the dyads at metaphase II; this divided and the two halves were equally distributed between the two poles. In 4% of the cells, the two halves moved to the same pole resulting in one of the four microspores having two fragments while the other three microspores were without any fragments.

Table 3. *Analysis of variance of PMC chiasma frequency between plants and between PMC's of plants of inbred lines in two seasons*

Souce of variation	Main season				Second season			
	DF	SS	MS	'F' Statistic	DF	SS	MS	'F' Statistic
Inbred A								
Between Plants	9	210.20	23.35	31.03*	9	116.10	12.90	33.55*
Between PMC's	19	416.10	21.90	29.10*	19	331.40	17.44	45.07*
Error (within Plants and within PMC's)	171	128.70	0.7526	–	171	65.70	0.3869	–
Total	199	755.0	–	–	199	513.20	–	–
Inbred B								
Between Plants	9	136.92	15.213	90.69*	9	58.95	6.551	22.99*
Between PMC's	19	217.92	11.47	68.39*	19	226.80	11.93	41.88*
Error (within Plants and within PMC's)	171	28.68	0.1677	–	171	48.75	0.2850	–
Total	199	383.52	–	–	199	334.50	–	–
Inbred C								
Between Plants	9	12.50	1.39	5.635*	9	36.4	4.044	8.80*
Between PMC's	19	117.60	6.19	25.09*	19	179.0	9.421	20.49*
Error (within Plants and within PMC's)	171	41.90	0.2467	–	171	78.6	0.4596	–
Total	199	172.0	–	–	199	294.0	–	–
Inbred D								
Between Plants	9	17.07	1.896	11.78*	9	25.65	2.85*	16.66*
Between PMC's	19	46.72	2.459	15.27*	19	32.20	1.70	9.94*
Error (within Plants and within PMC's)	171	27.53	0.161	–	171	29.05	0.171	–
Total	199	91.32	–	–	199	87.00	–	–

* Significant at 5% level.

The above two conditions, viz. the presence of extra chromosome and extra fragments, might be the consequence of a premeiotic error. Stickiness, reported in maize by Beadle (1933), if operating during the premeiotic stages, may lead to non-disjunction as well as breakage.

Desynapsis: In the inbred lines, A, B and C, desynapsis was observed. The desynaptic phenomena in the three inbred lines were similar except for the difference in degree, i. e., the number of univalents present in PMC's, which varied from 2 to 12 at diakinesis and metaphase I in the inbred A, whereas in inbred B and C the univalent number varied from 2 to 8 and 2 to 4, respectively (Fig. 6).

To study the inheritance of the desynaptic condition, selfed seed from the desynaptic plants was collected and progeny was raised. The inheritance did not follow any regular pattern in its segregation and thus it seems that the desynaptic condition might be the consequence of recombination of many genes, as was observed in rye by Rees (1955), rather than being under single gene control.

Persistent nucleoli: Normally, nucleoli in meiosis disappear by the end of diakinesis and reappear in telophase I. In inbred A in the main season, and in inbred B in the second season, one plant out of 20 plants in the former and one plant out of 25 in the latter showed the condition of persistent nucleoli, i. e. the presence of nucleoli at metaphase I and anaphase I. These nucleoli varied in size and number in the same plant. None of the progeny plants obtained on selfing showed persistent nucleoli (Fig. 5).

Differential condensation: This condition was observed in one plant out of 25 plants of inbred A during the main season. In a low frequency of PMC's, the condensation of the bivalents varied, i. e., some of the bivalents failed to undergo the normal prophase condensation and remained very relaxed while the other bivalents were normal in their prophase condensation. The number of retarded bivalents varied from 2 to 5 per PMC. This phenomenon was observed only at diplotene and diakinesis stages. The degree of condensation in a cell varied from bivalent to bivalent and also from diplotene to diakinesis. Generally, by the time these chromosomes reached metaphase I, they had caught up. The phenomenon of retardation was not specific to any chromosome pair in the PMC's as the number of retarded bivalents varied from cell to cell (Fig. 7). A similar phenomenon was observed in plants with more than four B-chromosomes, in a plant with two extra chromosomes deficient for short segments, and in plants raised from seed treated with Cupferron.

Analysis of F_1 hybrids:

Mean chiasma frequencies of the F_1 hybrids: The mean chiasma frequencies of all the six hybrids in both seasons transcended those of the greater parents, thus showing heterosis for chiasma frequency. Some of the hybrids, i. e., hybrids A × B and A × C, in the main as well as in the second season, had mean chiasma frequencies greater than those found in the heterozygous natural population plants. The mean chiasma frequencies for the other four hybrids were more or less the same as those for the heterozygous natural population (Table 1) (Fig. 8).

Variation between the hybrid families: The analysis of variance test showed differences among the six F_1 families in the main and the second season; the table value for '*F*' at 5% level (F_5, $9 = 3.48$) was greater than the observed '*F*' value (Table 4).

Variation between plants in hybrid lines: The analysis of variance tests showed the variation within all six hybrid lines to be significant in both the seasons since the observed '*F*' value was greater than the value from '*F*' tables (F_9, $45 = 2.10$) at 5% and 1% levels (Table 4).

Table 4. *Analysis of variance of PMC chiasma frequency between hybrids and between plants of hybrids in two seasons*

Source of variation	3	SS	MS	'F' Statistic
Hybrids in main Season				
Between Hybrid Families	5	5.11	1.022	38.71*
Between Plants	9	1.93	0.2145	8.125*
Error (within Hybrid Families and within Plants)	45	1.188	0.0264	—
Total	59	8.228	—	—
Hybrids in second Season				
Between Hybrid Families	5	5.22	1.044	19.08*
Between Plants	9	2.78	0.3089	5.646*
Error (within Hybrid Families and within Plants)	45	2.462	0.0547	—
Total	59	10.462	—	—

* Significant at 5% level.

Variation in mean chiasma frequency between PMC's in hybrid plants: The analysis of variance data showed that the table value for '*F*' was less than the observed '*F*' (F_{19}, $171 = 1.654$) at the 5% level of significance and hence the variation within each of the hybrid plants was significant (Table 5).

Comparison of inbreds and F_1 hybrids: When the mean values for chiasma frequency of the inbred lines and their F_1 hybrids were compared, the values of all the six hybrids, in the main and in the second seasons, were greater than the mean values of the respective participating parents (Table 1). The differences between the hybrids and their parents were tested by means of '*F*' test and the differences in variances were found to be significant, as the observed '*F*' value was found to be greater than the value from '*F*' tables (F_3, $5 = 5.41$) at 5% level.

When the heterozygotes are compared with their inbred lines, it can be seen that the F_1 families differ

Table 5. *Analysis of variance of PMC chiasma frequency between plants and between PMC's of plants of hybrid families in two seasons*

Source of variation	Main season				Second season			
	DF	SS	MS	'F' Statistic	DF	SS	MS	'F' Statistic
Hybrid A × B								
Between Plants	9	17.71	1.968	20.17*	9	10.70	1.194	18.91*
Between PMC's	19	17.81	0.9371	9.603*	19	24.85	1.308	20.71*
Error (within Plants and within PMC's)	171	15.09	0.0976	—	171	10.80	0.06316	—
Total	199	50.61	—	—	199	46.35	—	—
Hybrid A × C								
Between Plants	9	6.60	0.733	10.20*	9	5.8	0.6445	43.25*
Between PMC's	19	25.85	1.360	18.92*	19	27.0	1.421	95.75*
Error (within Plants and within PMC's)	171	12.30	0.0719	—	171	3.2	0.0149	—
Total	199	44.75	—	—	199	36.0	—	—
Hybrid A × D								
Between PMC's	9	4.35	0.4834	5.456*	9	4.5	0.5000	8.141*
Between Plants	19	13.1	0.6895	7.782*	19	21.6	1.1370	18.51*
Error (within Plants and within PMC's)	171	15.15	0.0886	—	171	10.5	0.06141	—
Total	199	32.60	—	—	199	36.6	—	—
Hybrid B × C								
Between Plants	9	13.8	1.533	16.60*	9	10.5	1.167	13.04*
Between PMC's	19	19.9	1.047	11.33*	19	19.7	1.037	11.59*
Error (within Plants and within PMC's)	171	15.8	0.0924	—	171	15,3	0.08948	—
Total	199	49.5	—	—	199	45.5	—	—
Hybrid B × D								
Between Plants	9	13.42	1.491	163.50*	9	12.95	1.439	13.71*
Between PMC's	19	20.62	1.085	119.00*	19	19.10	1.005	9.572*
Error (within Plants and within PMC's)	171	1.56	0.00912	—	171	17.95	0.1050	—
Total	199	35.60	—	—	199	50.90	—	—
Hybrid C × D								
Between plants	9	1.70	0.1889	3.895*	9	9.9	1.100	12.97*
Between PMC's	19	22.0	1.158	23.87*	19	9.1	0.4788	5.646*
Error (within Plants and within PMC's)	171	8.3	0.0484	—	171	14.5	0.0848	—
Total	199	32.0	—	—	199	33.5	—	—

* Significant at 5% level.

from their parents, not only in mean chiasma frequencies, but also in variation in the mean chiasma frequencies. The variability existing between the inbreds and their F_1 hybrids was measured in terms of the standard deviation (SD) and coefficient of variation (CV) and the results are presented in Table 1. When the CV of the F_1's were compared with those of their respective participating parents, the CV of F_1's were smaller than the CV of their parents. Because the inbred lines are homozygous, the differences between plants within inbred lines and between plants in F_1 families must be to a large extent non-heritable, resulting from fluctuations in the environmental conditions under which the plants were grown. This can be more clearly shown if comparisons between the inbred lines and their F_1's are made over two seasons, the stress and the non-stress seasons. The data presented in Table 1 for mean chiasma frequencies, with SD and CV of the inbred lines and their F_1's, again show that the effect of the environment is less in F_1's than in the inbred lines. It may be concluded that the environmental changes affect chiasma frequencies in homozygotes significantly more than in heterozygotes. The development of the heterozygotes in respect of chiasma frequency is more stable than that of the homozygotes under the same range of conditions.

The greater stability of development in the F_1 heterozygotes can also be shown if variation in mean chiasma frequencies between nuclei within plants are compared. The data obtained on variation for the inbred lines and their F_1 hybrids over two seasons clearly revealed that there is significantly less variation in chiasma frequencies between PMC's within F_1 plants than within inbred plants. This confirms that in heterozygotes the development of pollen mother cells is more uniform than in homozygotes under the same growing conditions.

Table 6. *The frequency of plants showing different meiotic abnormalities in the inbred lines in two seasons*

Meiotic abnormality	Number of plants showing each abnormality			
	A	B	C	D
		Main Season		
Desynapsis	2 (20)	1 (20)	—	—
Persistent nucleoli	1 (20)	—	—	—
		Second Season		
Trisomy	1 (25)	—	—	—
Desynapsis	6 (25)	2 (25)	1 (20)	—
Fragments	1 (25)	—	—	—
Persistent nucleoli	—	1 (25)	—	—
Differential condensation	1 (25)	—	—	—

The numbers given in the brackets denote the total number of plants scored for meiotic abnormalities.

Meiotic abnormalities in the inbred lines and their F_1 hybrids: Forced inbreeding in a normally outbreeding species may affect the efficiency of chromosome behaviour compared with that of population plants. In pollen mother cells at meiosis, this inefficiency may be considered to be a form of inbreeding depression (Rees, 1961). Relative sterility of the inbreds is one of the expressions of inbreeding depression and the contributory causes of sterility are reduced chiasma frequency and an increased proportion of structural and behavioural abnormalities. Thus, the increase in the number of structurally abnormal pollen mother cells in inbred plants may be taken as a manifestation of inbreeding depression at nuclear level. Therefore, the absence of abnormalities in F_1's may be regarded as a form of heterosis. In the present study, the F_1's did not show any meiotic abnormalities in either season and hence are considered heterotic.

Conclusions

Pennisetum typhoides, which is naturally a cross-pollinated species, showed the effects of drastic change in the breeding system under enforced inbreeding. All the inbred lines showed a mean chiasma frequency significantly lower than that in the natural population, and an increase in the variation in mean chiasma frequency. Also there was a decrease in the level of efficiency of chromosome behaviour during meiosis in PMC. All the inbred lines were not alike in these characters, some being less stable than others, and they differed genetically in the control of these characters. A study of the critical differences between inbred lines also revealed that the inbred lines were genotypically different.

The environmentally influenced effects on the chiasma frequencies of the inbred lines were 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 variances are considered as the measure of stability, the four inbred lines differ in their relative stability. As in rye and in maize, the inbreeding depression might depend upon the segregation of particular homozygous combinations rather than on some specific demerits of homozygotes.

When the inbred lines were crossed, all the F_1's attained a level of chiasma frequency and meiotic chromosome behaviour characteristic of that of the natural population. All the F_1's showed mean chiasma frequencies higher than those of their participating parents, thus exhibiting heterosis for chiasma frequency. Some of these F_1's showed chiasma frequencies higher than those in the natural populations. The variation in mean chiasma frequency between cells within the same plant in the F_1's again was smaller than that in the inbred lines. The smaller variation in heterozygotes, between PMC's, and between plants of the same family reflects greater stability in development in both seasons. Although this kind of variation is initiated by environmental fluctuations, the amount of variation exhibited depends on the particular genotype.

Heterozygous genotypes in general show less variation, i. e., show greater stability, than homozygotes. But this may not be directly dependent on the degree of hybridity in itself, because inbred lines, homozygous, show different degrees of stability. It appears that the high degree of developmental stability has been achieved by the action of natural selection for particular balanced genic combinations (Rees and Thompson, 1956).

Meiotic abnormalities which were observed in inbred lines were not present in F_1's. Whatever genetic mechanism that is controlling these characters is perhaps related to the heterozygosity and hence to the breeding system. In rye, according to Rees (1955a), "an outbreeding population, by virtue of the high average heterozygosity of its members, is genetically balanced and buffered against disadvantageous irregularities like structural abnormalities and poor pairing. This, genetically heterozygous, buffer has no doubt been built up encouraged by selection under natural conditions of outbreeding. Its breakdown coincides with the breakdown of the normal outbreeding system". With inbreeding, i. e., with increased homozygosity, a number of abnormalities emerge. The inbred lines differ in the form and distribution of these irregularities as a result of segregation; the chromosome behaviour is less efficient in the inbred lines and in this respect they differ one from another.

Acknowledgements

We are thankful to Prof. J. Venkateswarlu, Head of the Department of Botany, Andhra University, Waltair, for the facilities, and to Prof. T. V. Avadhani of Statistics Department for help in statistical analysis. The Junior author expresses her thanks to the U.G.C. for the award of a Junior Research Fellowship.

References

1. Beadle, G. W.: Further studies in asynaptic maize. Cytologia **4**, 269—287 (1933). — 2. Lamm, R.: Cytological studies on inbred rye. Hereditas **22**, 217—240 (1936). — 3. Müntzing, A., Akdik, S.: Cytological disturbances in the first inbred generation of rye. Hereditas **34**, 485—509 (1948). — 4. Rees, H.: Genotypic control of chromosome behaviour in rye. I. Inbred lines. Heredity **9**, 93—116 (1955a). — 5. Rees, H.: Heterosis in chromosome behaviour. Proc. Roy. Soc., B, **144**, (1955b). — 6. Rees, H.: Genotypic control of chromosome form and behaviour. Bot. Rev. **27**, 288—318 (1961). — 7. Rees, H., Thompson, J. B.: Genotypic control of chromosome behaviour in rye. III. Chiasma frequencies in homozygotes and heterozygotes. Heredity **10**, 409—424 (1956). — 8. Sybenga, J.: Inbreding effects in rye. Z. Vererb.-Lehre. **89**, 338—354 (1958).

Received March 19, 1971
Communicated by M. S. Swaminathan

Dr. J. V. Pantulu
V. Manga
Department of Botany,
Andhra University,
Waltair (India).