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TRANSMISSION OF DEFICIENT GAMETES BY MONOSOMICS OF *AVENA SATIVA* L.

H.M.I. HAFIZ

Department of Botany, Punjab University, New campus, Lahore, Pakistan.

Abstract

Parental monosomics (2n-1=41) derived from the cultivars Garry (WM 2-1) from Canada and Borreck (GM 1-1) from West Germany, their monosomic F_1 hybrids and BC_1 - BC_4 to Sun II were used to study the transmission of deficient gametes. The frequency for functional 20-chromosome male gametes was lower in the homozygous than heterozygous monosomics. The 40-, 41- and 42-chromosome progenies in selfed monosomic individuals depend upon the proportion of deficient (2n-1) but functional male gametes. The correlation between the proportion of 20-chromosome gametes produced and the proportion that function is significant ($r = -0.86$).

Introduction

The common cultivated oat, *Avena sativa* (2n=6x=42=AACCDD), because of its polyploid nature, can withstand deficiency not only at the sporophytic but also at gametophytic level. The monosomic individuals exhibit meiotic instability the first manifestation of which is the partial asynapsis at metaphase I. Consequently deficient gametes are produced in disproportionately high frequency. An estimate of the proportion of n and n-1 spores may be obtained by determining the frequency of spore tetrads possessing micronuclei. Theoretically an individual with (2n-1) chromosomes produces (n) and (n-1) gametes in equal frequencies. Likewise (2n) and (2n-1) individuals are expected to be produced in equal frequency from (2n-1) and (2n) crosses. Furthermore, (2n-1) plants should result in (2n), (2n-1) and (2n-2) progeny in 1:2:1 ratio when selfed. However, these expected ratios are never realised and the reasons for the departure are indeed varied.

The transmission of deficient gametes in the monosomics of *Avena sativa* has been shown to be affected by the genetic background (Rajhathy & Thomas, 1974; Hafiz & Thomas, 1978). In the present study two monosomic lines originally isolated from the cultivars Garry and Borreck were backcrossed to Sun II and the data are presented on the transmission of deficient gametes based on the comparison of the 40-, 41- and 42-chromosome progenies of the selfed monosomic parents, their F_1 and BC_1 to BC_4 to Sun II.

Materials and Methods

The aneuploid lines isolated from the cultivars Garry and Borreck, the derivatives

of common oat, and hexaploid Sun II were employed in the present investigation. The sources of these cultivars, their F_1 and other hybrids in the backcrossing programme to Sun II involving the monosomic lines have been described earlier (Hafiz, 1977a).

To establish the chromosome number of seeds, they were allowed to germinate on thoroughly soaked filter papers in Petri dishes which were kept at constant temperature (22^{o} C). Roots were excised when approximately 8-10 mm long; pretreated in ice-chilled water ($0\text{-}2^{o}$ C) for 24 hours; fixed in absolute alcohol: acetic acid (3:1) for at least 1½ hours (Tsunewaki & Jenkins, 1960); hydrolysed in N HCl at 60^{o} C for 10 minutes; stained with Feulgen reagent and finally 1-2 mm long root from the tip side squashed in 1% acetocarmine (Morrison, 1953; Melynk & Unrau, 1961). After determining the chromosome numbers, the required seedlings were transplanted individually to 12 cm. diam. pots.

The 40-, 41 and 42-chromosome conditions of various individuals were confirmed at meiosis of pollen mother cells (PMCs) by the method described earlier (Hafiz, 1977a). Plants were grown in the green house that was heated during the winter months and the supplementary light was provided from Mercury Vapour Lamps.

Results

Chromosome counts were made of the root tips of the progenies of monosomic parents, WM 2-1 and GM 1-1, the monosomic F_1 and BC_1-BC_4 generations to Sun II. At least 50 seeds from each hybrid and parent were analysed and the number of nullisomics (2n-2=40), monosomics (2n-1=41) and disomics (2n=42) are shown in Table 1. The mitotic chromosome number of nullisomics was confirmed at meiosis.

Assuming that the proportion of (n) and (n-1) female gametes is the same as the calculated values for the male gametes, it is possible to calculate the expected proportion of euploid, monosomic and nullisomic progenies when monosomic are selfed. It is also assumed that the deficient and euploid gametes are equally effective in their ability to function during fertilisation. Expected values for disomics, monosomics and nullisomics based on the proportion of (n) and (n-1) gametes formed are calculated as below

♂ Gametes → / ↓ ♀ Gametes	n=21 (0.08)*	n-1=20 (0.92)*
n=21 (0.08)	2n=42 (0.0064)	2n-1=41 (0.0736)
n-1=20 (0.92)	2n-1=41 (0.0736)	2n-2=40 (0.8464)

*Proportion of (n) and (n-1) male gametes produced by the monosomic WM 2-1 (Hafiz, 1977b).

Table 1. The progenies of selfed monosomic parents, monosomic F_1 and backcross generations to Sun II in the Garry and Borreck series.

Monosomic line		Parent	F_1	BC_1	BC_2	BC_3	BC_4
Garry (WM 2-1)	No. of plants analysed	50	55	50	54	53	54
	Nullisomics (2n-2=40)	0.0	6	11	5	57	4
	Monosomics (2n-1=41)	48	47	35	46	44	45
	Disomics (2n=42)	2	2	4	3	2	5
	% Nullisomics	0.00	10.90	22.00	9.26	13.21	7.4
Borreck (GM 1-1)	No. of plants analysed	52	52	57	51	48	52
	Nullisomics (2n-2=40)	2	6	7	3	5	2
	Monosomics (2m-1=41)	47	42	48	45	38	48
	Disomics (2n=42)	3	4	2	3	5	2
	% Nullisomics	3.85	11.54	12.28	5.88	10.42	3.85

A comparison of observed frequencies of disomics, monosomics and nullisomics of each generation and the calculated frequencies based on the proportion of nullisomic (n-1) gametes produced (Table 2) clearly shows that the proportion of nullisomic progeny was much lower than expected. However, the expected values, at least in some cases, were as high as 84%. In none of the progenies did the observed values for 40-chromosome plants approach the calculated expectation. It is also clear from Table 2 that the number of monosomics produced is high and consequently the values for nullisomics and disomics are low. Both the monosomic lines – Garry and Borreck – their F_1 and BC_1-BC_4 generations to Sun II show similar pattern as far as the segregation of disomics, monosomics and nullisomics in selfed monosomics is concerned.

The proportion of nullisomic individuals was higher in the progenies of F_1 and BC_1 generations as compared with that of original monosomic parents. In both the lines, BC_1 yielded more 40-chromosome progeny as compared with that of F_1. Nullisomics were less frequent in the progenies of BC_2 followed by a slight increase in BC_3. In BC_4 of Garry and Borreck the respective observed values for nullisomics were 7.41 and 3.85% compared with the original corresponding values 0.00 and 3.85% in WM 2-1 and GM 1-1.

Table 2. Expected and observed values (%) for the disomics, monsomics and nullisomics progenies in selfed monosomics in different generations.

Monosomic Line			P	F_1	BC_1	BC_2	BC_3	BC_4
	Disomics	Expected	0.64	4.84	7.29	2.89	4.84	0.64
Garry	(2n=42)	Observed	4.00	3.64	8.00	5.45	3.77	9.26
(WM 2-1)	Monosomics	Expected	14.72	34.32	39.42	28.22	34.32	14.72
	(2n-1=41)	Observed	96.00	85.45	70.00	85.19	83.02	83.33
	Nullisomics	Expected	84.00	60.84	53.29	68.89	60.84	84.64
	(2n-2=40)	Observed	0.00	10.91	22.00	9.26	13.22	7.41
Borreck	Disomics	Expected	1.96	3.61	–	2.86	6.25	2.89
(GM 1-1)	(2n=42)	Observed	5.77	7.69	3.51	5.88	10.41	3.84
	Monosomics	Expected	24.08	30.78	–	28.42	37.50	28.42
	(2n-1=41)	Observed	90.38	80.77	84.21	88.24	79.17	92.31
	Nullisomics	Expected	73.96	65.61	–	68.69	56.25	58.69
	(2n-2=40)	Observed	3.85	11.54	12.28	5.88	10.42	3.85

All the observed values for nullisomics of BC generations have been plotted together with the curve for the theoretical values for homozygosity in the backcrosses (Fig. 1). It seems that, with the recovery of homozygosity, there is a decrease in the frequencies of nullisomics present in the progenies of monosomic plants when selfed. It is of interest to note also that, although WM 2-1 did not yield nullisomics, its BC_4 to Sum II gave 7.41% 42-chromosome individuals. However in GM 1-1 the proportion of nullisomic progeny in BC_4 was identical with that of the original line. It is also obvious from the comparison of the observed frequencies of nullisomic, monosomic and disomic progenies and their calculated frequencies based on the proportion of (n) and (n-1) gametes formed that although the majority of gametes are deficient for the monosome they donot function in the process of fertilisation with the same frequency as the normal gametes.

The per cent of deficient gametes that function were calculated from the observed frequencies of nullisomics and disomics by the application of the following formula:

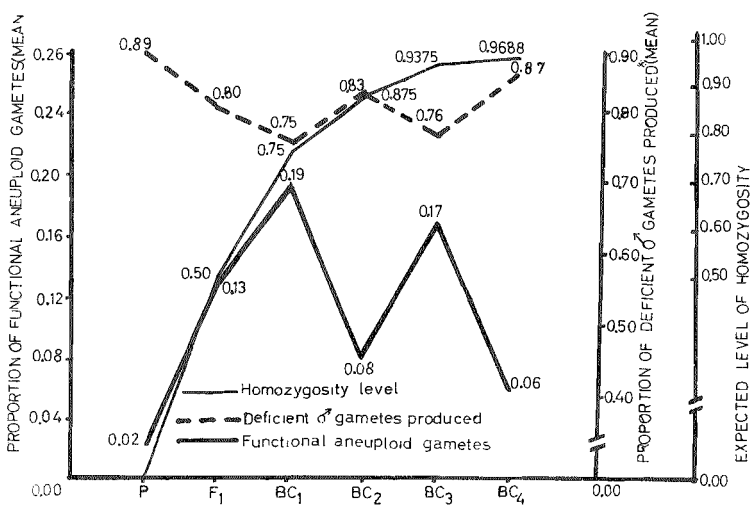
$$2P_{20} = (N + 1\text{-}U) \pm \sqrt{(U - 1\text{-}N)^2 - 4N}$$

where

P_{20} is proportion of 20-chromosome functional gametes

N is proportion of nullisomic offspring, and

U is proportion of disomic offspring.



*Hafiz 1977b

Fig. 1. Relationship between the proportion of deficient male gemetes produced, proportion of functional aneuploid male gemetes and expected values for homozygosity in selfed monosomic individuals.

Table 3. Proportions of functional 20-chromosome male gametes in the progenies of monosomic original parents, their monosomic F_1 hybrids and monosomics of subsequent BC generations.

Generation → / Line ↓	Parent	F_1	BC_1	BC_2	BC_3	BC_4
Garry (WM2-1)	0.00	0.12	0.25	0.10	0.14	0.08
Borreck (GM 1-1)	0.04	0.13	0.13	0.06	0.21	0.04
Average	0.02	0.13	0.19	0.08	0.17	0.06

The frequencies of functional (n-1) male gametes are presented in Table 3. The minimum and maximum proportions of deficient male gametes that function were recorded in the original Garry and its monosomic BC_1, the values being 0.00 and 0.25, respectively. In the Borreck series, the corresponding values are 0.04 and 0.13. Moreover, the proportions of functional (n-1) pollens in BC_3 of Garry as well of Borreck were higher compared to those of the preceeding and following BC generations. It is also quite obvious that, with the exception of BC_3 monosomic progeny, the proportion of functional 20-chromosome pollens exhibits a gradual fall from BC_1 to BC_4 in both the series. It is apparent too that a high proportion of nullisomics in the progenies in selfed monosomics (cf. Tables 1 and 2). Fig. 1 illustrates the inconsistent pattern recorded for the functional (n-1) pollens in the monosomic progenies of BC_1 to BC_4 generations.

The correlation between the proportions of 20-chromosome gametes produced and those functioned was calculated, after all the values were transformed to angles expressed in degrees corresponding to arcsin $\sqrt{}$ percentage (Bliss, 1937). The correlation coefficient was -0.86 ± 0.17 with d.f.=9 (significant at the 0.1% level (Fig. 2). Furthermore, in Fig. 1 where the curve for the expected per cent of homozygosity through successive BC generations has been represented along with the mean proportions of deficient gametes produced and those functioning when monosomics were selfed, it is apparent that the frequency for the functioning 20-chromosome pollens is lower in the homozygous than in heterozygous monosomics. It is also clear from the observations that 40-, 41- and 42-chromosome offspring in the selfing monosomic individuals depend upon the proportion of aneuploid gametes that were able to function rather than the proportion of (n-1) gametes produced.

Discussion

The monosomic oats exhibit partial asynapsis at metaphase I, thus leading to the production of aneuploid and normal gametes in disproportionate frequencies (Nishiyama, 1931; Philp, 1935, 1938; McGinnis & Taylor 1961; Lafever & Patterson, 1964; Hacker,

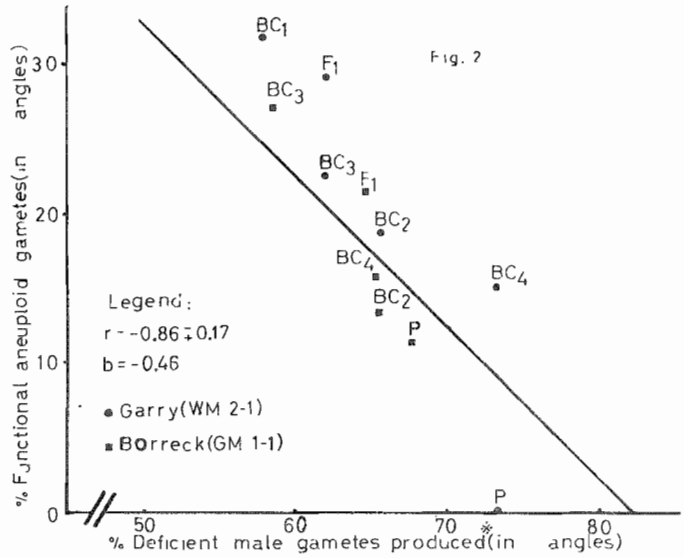


Fig. 2. Regression line fitted to the data of Tables 1 and 3 (the values have been converted to angles).

1965; Gauthier & McGinnis, 1965; McGinnis & Lin, 1966; Singh & Wallace, 1967; Nishiyama et al., 1968, Hafiz 1977a,b; Hafiz & Thomas, 1978). Another parameter of paramount importance of such individuals is the transmission of 20-chromosome gametes which are studied by their manifestation in the segregation ratio of nullisomics, monosomics and disomics in the progenies of selfing monosomics of different genetic backgrounds. The frequencies of nullisomics (2n-2=40) in the progenies of different monosomic lines as reported previously have been summarised in Table 4. It is clear that there was a considerable range in the frequency of nullisomics produced by different monosomics when selfed. In the instances where the frequency of nullisomics was high it was assumed that there was no certation between 20- and 21-chromosome pollens (Philp, 1935, 1938; McGinnis & Taylor, 1961; McGinnis & Andrews, 1962 for mono-21, McGinnis et al., 1968 for mono-14; McGinnis & Lin, 1966 for mono-15). However the assumption was disputed by O'Mara (1961), Change &Sadanaga (1964) and Hacker (1965) because of their results based on the actual transmission rate of 21 and 20-chromosome pollens from crosses of monosomics with the normal (42-chromosome) varieties using monosomics as male parents. In the present investigation, gametes, independent of their number and lacking one or the other chromosome in their haploid complement, show the ability to function in the process of fertilisation. In most of the monosomics under investigation, nullisomics were recorded. The observed values for nullisomics ranged from 0.00 to 22.0% (Table 2). The frequency of the nullisomic progeny could be influenced by the following factors:

a) reduced viability of deficient gametes,

b) certation between 20- and 21-chromosome gametes,

c) low competitive ability of (n-1) pollen compared with the (n) pollen,

d) reduced viability of aneuploid zygotes, and

e) reduced viability of (2n-2) zygotes (Khush,-1975).

The deficient gametes are produced in disproportionately high frequency due to one or the other reason. The results from monosomics of wheat and oat indicate that (n-1) spores are as viable as the (n) spores (Morrison, 1953; Sears, 1954; Change & Sadanaga, 1964; Tsunewaki, 1964; Hacker, 1965). Change & Sadanaga, (1964) and Hacker (1965), from competitive (2n-1 ♂ x 2n ♀) and non-competitive (2n-1 ♀ x 2n ♂) pollens, reported that the transmission frequency of 20-chromosome pollen was reduced or almost none in the competitive pollination involving (n) and (n-1) pollens. The degree of competition, however, varied in different monsomic lines. Competition, similar to mentioned above occurred also when monsomics were allowed to self (Hacker, 1965). He concluded that the complete absence of 40-chromosome progeny in some monosomic lines of *A. sativa*

Table 4. Number of monosomic lines with different frequencies of nullisomics in their progenies.

Authority	Frequency of nullisomics in progenies of monosomic lines of different origins.				Plant analysed
	Class A 50% ror more	Class B 10-49%	Class C less than 9%	Class D 0.0%	
					Avena fatua
Nishiyama (1931, 1933)	–	2	–	3	
Philp (1935)	1	–	–	–	*A. sativa*
" (1938)	1	–	–	–	"
Costa-Rodrigues (1954)	–	2	3	–	"
O'Mara (1951)	2	1	–	1	"
McGinnis and Taylor (1961)	1	–	–	–	"
McGinnis (1962)	1	1	1	1	"
McGinnis and Andrews (1962)	1	–	–	–	"
McGinnis *et al.* (1968)	1	–	–	–	"
McGinnis and Lin (1966)	1	–	–	–	"
Gauthier and McGinnis (1965)	–	1	–	–	"
Ghang and Sadanaga (1964)	–	–	2	4	"
Lafever and Patterson (1964)	1	–	–	–	"
Singh and Wallace (1967)	1	2	–	1	*A. Byzantina*
Nishiyama *et al.*	–	1	–	16	"
Present study	–	6	2	–	*A. sativa*
	Number of monosomic lines				

was fully dependent on the reduced functioning ability of 20-chromosome pollens. Pavek (1965) reached essentially a similar conclusion. In some series of monosomic hybrids studied in the present investigation, the lines which were heterozygous produced nullisomics in higher frequency than the corresponding homozygous lines. The competitive ability of (n-1) pollen is the prime factor influencing the segregation of 40-41- and 42-chromosome progenies when monosomics were selfed. It seems that the heterozygous genetic background improves the competitive ability of deficient gametes (Table 2).

Chang & Sadanaga (1964) did not find nullisomics in the progenies of most of the selfing monosomics, viz., Mono-A, -B, -D and -F in the cultivar Cherokee of *A. sativa*. However, in F_2 populations of crosses between mono-C and three other varieties -C.I. 7451, Victoria and Markton- a high incidence of nullisomics was observed. They attributed the general low frequency of nullisomics in the progenies of selfing monsomics to varietal differences and the deleterious effect of X-rays (six monosomics employed in their analysis were chosen from an X-rays treated population). In addition to the reduced functioning ability of pollens, several workers have postulated the existence of zygotic lethality or the elimination of nullisomics which would be partly responsible for their decreased frequency (Huskins, 1927; Nishiyama, 1931, 1933; Costa-Rodrigues, 1954; McGinnis, 1962; Gauthier & McGinnis, 1965). Although the functioning ability of deficient male gametes from monosomics is evidently much inhibited, the observations on young seeds or ovaries made Nishiyama et al. (1968) to suggest that the young embryos might abort in the early stages of development.

Sears (1944, 1954), in his extensive studies on wheat monosomics, found low frequencies of nullisomics (0.9 to 7.6%) in the progenises of 21 monosomic lines. Earlier studies on the progenies of pentaploid *Triticaum* hybrids (Kihara, 1924) and triploid *Avena* hybrids (Nishiyama, 1934) revealed that chromosomal constitution had serious and permanent consequences, since the complete parental type genome cannot be reconstituted as was the case when monosomics were selfed. The nullisomic condition might result in a non-viable combination of chromosomes. The degree of reduced viability of the zygote could be attributed to the absence of each pair of chromosome thus reducing the fitness of the genotype in a differential manner. In the present investigation it is obvious that the nullisomics are viable in the progenies of selfing monosomic parents, F_1 and BC generations.

The genetic background influences the transmission rate of the aneuploid gametes (Hafiz & Thomas, 1978). In general, the higher the degree of hterozygosity the higher the rate of transmission of (n-1) pollen in comparison with plants nearly homozygous. It is, however, impossible to be specific as to how the genetic background of the monosomic lines influences the transmission rate of deficient gametes. The monosome, moreover, responsible for the deficiency in pollens, behave differently in different genetic background. While McGinnis & Taylor (1961) reported a nullisomic frequency of 63% for the chromosome 21 in the monosomic progeny in advanced generations of crosses R.L. 1574 x Ripon. Hacker (1965) could obtain only 0.5% nullisomics for the same chromosome in comparable generations in Sun II background. In the present study, the monoso-

mics belonging to Garry did not produce nullisomics while in BC_4 to Sun II 7.4% of the progeny obtained by selfing the monosomics were nullisomics. Alston & Jones (1968) and Kaltsikes et al. (1970) also provided evidence on the effect of genetic background on the transmission rate of deficient pollens. They reported that the univalent transmission rate differed among the pentaploid wheat hybrids of different genetic backgrounds. Makino (1974) arrived at a similar conclusion by employing two different kinds of pentaploid wheat hybrids. According to him, two factors responsible for the transmission pattern of univalents are the elimination of the chromosome at the gametogenesis and preferential fertilisation of genomically balanced gametes. Moreover, he suggested that the transmission of the univalent chromosome was under the control of at least two major genes in the pentploid wheat. The monosomic and, in some cases, nullisomic plants are viable and fertile which facilitates the monosomic analysis in the genetic studies, especially the gene-chromosome association, of the polyploid species (Thomas & Mytton, 1970; Sadanaga, 1975; Hafiz, 1978a,b,c).

Variation in the transmission rate of deficient gametes could thwart the use of monosomic analysis to locate genes on the specific chromosomes in *A. sativa,* because in monosomic analysis the gene in question should be effective in the hemizygous state so that the euploid and monosomic individuals are identified for the trait under study. If the proportion of (2n-2) individuals in the self progeny is excessive and does not deviate from the expected proportion of recessive genotypes in the F_2 of the corresponding hybrids it would be impossible to identify the monsome involved. In that case the progeny with the null effect have to be ascertained as being nullisomic by means of chromosome counting. The abnormally high transmission of nullisomics pollen would render mononsomic analysis completely ineffective unless it was accompanied by chromosome counts.

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