Theor Appl Genet (1985) 69:367–373

Micronuclei frequency and character coherence in *Avena sativa* L./*A. fatua* L. crosses

J. J. Luby, D. D. Stuthman and R. L. Phillips
Department of Agronomy and Plant Genetics, University of Minnesota, St. Paul, MN 55108, USA

Received May 15, 1984; Accepted May 26, 1984
Communicated by P. L. Pfahler

Summary. The use of micronuclei frequency per microspore quartet (MF) has been proposed to indicate the relative reduction in chromosome homology among interspecific oat (*Avena* L.) hybrids. Hybrids with lower MF would presumably undergo greater genetic recombination, providing greater opportunity for breaking linkages that contribute to association, or coherence, of desirable and undesirable characters in progenies. Microspore quartets from 63 *A. sativa*/*A. fatua* hybrids were observed. Character coherence was examined in progenies of the four hybrids with the highest MF (2.22 to 2.82 micronuclei/quartet) and four hybrids with the lowest MF (0.23 to 0.31 micronuclei/quartet) to determine whether a relationship existed between MF and character coherence. Coherence of seed disarticulation with quantitative characters that differentiate the parental species was more frequent in high MF crosses as was expected if high MF is indicative of reduced recombination. However, incidence of coherence between seed color and the quantitative characters was not related to MF differences among the crosses. Likewise, the degree of coherence among the quantitative characters, as measured by coefficients of concordance, was not associated with differences in MF among the crosses. Thus, coherence of the characters studied was not associated consistently with differences in MF.

Key words: Oat – Introgression – Genetic diversity – Interspecific cross – Recombination

Introduction

Introgression has been used to introduce genes from wild hexaploid oats (*Avena sterilis* L. and *A. fatua* L.) into cultivated oats, (*A. sativa* L.). *A. sterilis* has contributed genes for crown rust (*Puccinia coronata* Cda. f. sp. *avenae* Fraser and E. Led.) resistance (Frey and Browning 1976a, b), and increased grain yield (Frey 1976), groat protein percentage (Frey 1977) and groat oil percentage (Frey et al. 1975). *A. fatua* has contributed rust resistance and arid-region adaptation (Suneson 1967a), and earliness and rapid growth (Suneson 1967b) to cultivars developed in California. Burrows (1970) transferred the seed dormancy of *A. fatua* to *A. sativa* to develop a spring-type oat that could be fall planted, would remain dormant through the winter, and germinate in early spring.

Introgression has been hindered in several cases by associations of desirable with undesirable traits from the wild parent in cultivated/wild oat progenies. High groat protein percentage of *A. sterilis* was associated with shattering and dark seed color (Campbell and Frey 1972; Lyrene and Shands 1975), and with lemma pubescence, thin groats, and low groat percentage (Lyrene and Shands 1975). Campbell and Frey (1972) suggested that such associations might be due to linkage.

Linkages in cultivated/wild oat hybrids could be enhanced by reduced pairing between homologous chromosomes. McMullen et al. (1982) observed meiotic irregularities in *A. sativa*/*A. sterilis* hybrids including multivalents and, more frequently, univalents that eventually were manifest as micronuclei at the quartet stage of pollen development. Frequencies of meiotic irregularities varied among the crosses, suggesting that recombination might also vary. Among the crosses, micronuclei frequency (MF) was positively correlated with the frequency of diakinesis univalents, metaphase I univalents, and anaphase I laggards. Hence, McMullen et al. (1982) proposed that MF might be indicative of relative reduction in chromosome homology and genetic recombination among interspecific hybrids. Hybrids with low MF would be expected to undergo greater recombination and provide a greater opportunity for breaking undesirable character associations. Because the quartet stage of pollen development is long in oats and micronuclei stain darkly, MF is also easily determined.

The restriction of character recombination, or coherence, has long been recognized in natural hybrid plant populations (Clausen and Heisey 1960). Anderson (1939) attributed coherence to several factors including gametic or zygotic elimination, pleiotropy, and linkage. In addition, Smith (1950) observed developmental restrictions on dissociation of ontogenetically related traits.

Anderson (1949) proposed that the degree of recombination in segregating generations of interspecific crosses could be examined by determining the degree of multiple correlation among traits that distinguish the parental species. According to Anderson (1949) segregants are envisioned as occupying a "narrow spindle" (or ellipsoid) through the center of a multidimensional cube whose axes measure characters differentiating the parents. Parents occupy opposite apices of the cube.

Goodman (1966) proposed methods to measure the width of Anderson's recombination spindle. These methods allow comparison of character recombination or coherence in progenies from several interspecific hybrids. The first measure of spindle width is Kendall's coefficient of concordance (W) which measures the degree of multiple correlation among ranked characters. Two additional measures of spindle width may be used if characters are assumed to be distributed at least approximately multinormally. Goodman's multinormal coefficient of concordance (Y) is an analog of W using product-moment correlations in place of rank correlations. Goodman's parental coefficient of concordance (Z) uses product-moment correlations weighted by the difference between the parents standardized by the phenotypic standard error of the progeny population for each trait.

The objectives of our study were to determine 1) whether variation for micronuclei frequency existed among *A. sativa/A. fatua* hybrids and 2) whether differences in MF among *A. sativa/A. fatua* hybrids were related to differences in the degree of character coherence in their progenies.

Materials and methods

Crosses were made between the nine *A. sativa* lines used by McMullen et al. (1982) and seven randomly selected *A. fatua* accessions from the USDA Northern Plains collection described by Rines et al. (1980). *A. sativa* lines were used as female parents. Microsporocytes from one F_1 plant from each cross were collected, fixed and stained as described by McMullen et al. (1982). From 50 to 200 microspore quartets were observed for each of the crosses. Micronuclei frequency (MF) was determined as total number of micronuclei divided by the number of observed quartets. Based on microspore quartet observations, the four crosses with the highest MF (HMF crosses) and the four crosses with the lowest MF (L,F crosses) were selected, without regard to parentage, for further evaluation (Table 1).

Approximately 50 progeny lines per cross were derived from random F_2 plants by single-seed advance through the F_4 generation (Table 1). Parents and progeny lines were evaluated in the field at St. Paul, Minnesota. The parental seed was derived from the individual plants used to make the crosses. Progeny lines were evaluated in the F_5 generation in 1980 and the F_6 generation in 1981.

Parents were planted in a preliminary experiment in the summer of 1979 to determine which characters should be evaluated to examine coherence in the progeny. Agronomic and morphological characters were chosen that 1) seemed to consistently differentiate *A. sativa* parents from *A. fatua* parents, 2) appeared highly heritable, and 3) could be conventiently measured. The characters are listed in Table 2.

Table 1. *A. sativa/A. fatua* crosses with high and low micronuclei frequency (MF) and the number of evaluated progeny lines

Cross designation	Parents		MF	No. of progeny lines evaluated	
	A. sativa	*A. fatua*		1980	1981
High MF					
1	'Jaycee'	Af1223	2.62	46	50
2	'Noble'	Af565	2.22	49	50
3	'Noble'	Af573	2.37	37	50
4	'Tippecanoe'	Af117	2.82	45	50
Low MF					
5	'Otee'	Af206	0.28	48	50
6	'Otee'	Af565	0.31	46	50
7	'Stormont'	Af2068	0.27	20	49
8	'Tippecanoe'	Af1223	0.23	44	50

Parents and progeny lines were planted on 28 April 1980 and 18 April 1981 in hill plots on 30×60 cm centers at 25 seeds per hill in a randomized complete block design. Three replications were planted in 1980 and six replications in 1981. Three replications were sampled to measure second-leaf area and panicle traits in 1981, while the remaining three replications were harvested for grain. At 12 to 14 days after heading, each plot was covered with a plastic mesh bag to collect shattering seed. At maturity, plants in plots were cut 3 to 5 cm above ground level and dried.

Grain samples from two replications in each year were classified for seed disarticulation habit and seed color and used to determine 100-seed weight. Seed color classes were light (white or yellow) and dark (grey, brown or red). All *A. fatua* parents had shattering, dark-colored seed. All *A. sativa* parents had nonshattering, light-colored seed.

In 1981, grain samples were mechanically dehulled to determine groat percentage. Groat oil percentage was then determined by nuclear magnetic resonance at the Department of Agronomy, University of Illinois, Urbana, Illinois.

The two growing seasons were distinctly contrasting. Hot, dry conditions prevailed in 1980 while cool temperatures and adequate rainfall occurred in 1981. High winds associated with a thunderstorm on 15 July 1980 caused lodging of the entire experiment. In both years, plots were sprayed with maneb+zineb at four- to seven-day intervals to prevent crown rust infection. Nevertheless, infection was heavy by the end of the 1980 season.

In 1980, some genotypes showed poor emergence due to seed dormancy and the number of plants emerged at ten days after planting was recorded for each plot. In 1981, seeds of all genotypes were soaked 10 min in an acetone solution containing 50 ppm giberellin-4+7 : 50 ppm benzyladenine : 10 ppm ethephon, approximately 24 h before planting to break dormancy and promote germination (Taylor and Simpson 1980; Adkins and Ross 1981). Uniform emergence was observed in 1981.

Drought, rust, lodging, and the effect of dormancy in reducing stands of several genotypes in 1980 contributed to

Table 2. Traits studied for character coherence

Character	Description
Quantitative	
1. Harvest index	Grain yield ÷ bundle weight
2. Heading date	–
3. Height	–
4. Growth habit	Vegetative growth habit: Rated 1 = erect to 5 = prostrate
5. Panicle length	Mean of five panicles/plot
6. Spikelets/panicle	Mean of five panicles/plot
7. Nodes/panicle	Mean of five panicles/plot
8. Second leaf area	Area of the leaf below the flag leaf. Mean of five leaves/plot
9. 100-seed wt	Weight of 100 seeds
10. Seeds/panicle	Grain yield ÷ 100-seed weight ÷ (No. of panicles/plot)
11. Emergence	No. of plants/plot emerged at ten days after planting
12. Groat %	Groat weight as % of seed wt
13. Groat oil %	Oil weight as % of groat wt
Qualitative	
Seed disarticulation	Shattering, nonshattering
Seed color	Dark, light

Table 3. Micronuclei frequency in *A. sativa*/*A. fatua* hybrids

A. sativa parent	*A. fatua* parent							*A. sativa* parent	
	'Af206'	'Af565'	'Af1223'	'Af2068'	'Af573'	'Af1274'	'Af117'	$\bar{x}$	s^2
'Stormont'	0.65	0.26	0.37	0.27	1.10	1.01	0.53	0.60	0.12
'Otee'	0.28	0.31	0.46	0.48	0.96	0.97	1.39	0.69	0.18
'Clintland 64'	0.67	0.48	0.46	0.45	0.72	1.19	1.09	0.72	0.09
'Tippecanoe'	0.55	0.46	0.23	0.38	0.60	0.55	2.82	0.80	0.81
'Garland'	0.83	0.50	0.67	0.65	1.04	1.09	1.08	0.84	0.06
'MN67231'	0.22	0.31	0.41	0.80	1.03	1.38	1.91	0.87	0.39
'MN67201'	0.52	0.88	0.65	1.18	1.64	1.20	1.41	1.07	0.16
'Jaycee'	0.98	0.88	2.62	1.30	1.57	1.32	0.63	1.33	0.42
'Noble'	0.61	2.22	1.44	2.16	2.37	2.29	0.74	1.69	0.58
								all hybrids	
A. fatua $\bar{x}$	0.59	0.70	0.81	0.85	1.22	1.22	1.29	$\bar{x} = 0.97$	
Parent s^2	0.06	0.38	0.58	0.37	0.30	0.22	0.52	$s^2 = 0.38$	

large genotype-by-year interactions. Therefore, analyses were conducted for each year separately.

Two approaches were used to detect differences in coherence between HMF and LMF crosses. First, associations of the seed morphology traits with the quantitative traits were studied by grouping progeny lines in each cross by their disarticulation habit or seed color (Lyrene and Shands 1975). Only nonsegregating lines were included. Means for the quantitative characters were computed for each group in each cross and compared by a *t*-test using the pooled experimental error for each trait.

The second approach used Goodman's (1966) measures of recombination spindle width to determine coherence among quantitative characters for each cross. Following Goodman, Kendall's coefficient of concordance (W) was calculated for each cross as follows:

$$W = \bar{p}\,(m-1)/m + 1/m$$

where $\bar{p}$ is the average of phenotypic Spearman rank correlation coefficients for all pairs of m traits. Goodman's multinormal coefficient of concordance (Y) and parental coefficient of concordance (Z) were computed as follows:

$$Y = \bar{r}\,(m-1)/m + 1/m$$

where $\bar{r}$ is the average of phenotypic product-moment correlation coefficients for all pairs of m traits, and:

$$Z = 1 - \left(\sum_{k=1}^{n} D_k^2\right)/[m\,(n-1)]$$

where n is the number of progeny lines from the cross and

$$\sum_{k=1}^{n} D_k^2 = (m-1)\,(n-1) - (n-1) \sum_{\substack{i=j \\ i \neq j}}^{m} \sum_{j=1}^{m} a_i\, a_j\, r_{ij}$$

where r_{ij} is the phenotypic correlation between traits i and j in the population, and

$$a_i = (d_i/s_i)/\left[\sum_{i=1}^{m} (d_i/s_i)^2\right]^{1/2}$$

where d_i is the difference between the parents of the population for trait i, and s_i is the phenotypic standard error of the

Table 4. Coherence of quantitative traits with seed disarticulation habit determined by differences between progeny disarticulation classes

Cross	No. of lines				Harvest index		Heading date		Height		Growth habit		Panicle length		Spikelets/ panicle	
	Nonshattering		Shattering													
	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981
HMF																
1	17	17	24	28	C	–	C	–	–	–	–	–	–	–	C	–
2	26	26	18	19	C	–	–	–	–	–	C	–	–	–	–	–
3	24	29	11	17	–	–	–	C	–	–	–	–	–	C	–	–
4	18	21	23	25	–	–	–	–	–	–	–	–	–	–	–	–
LMF																
5	23	24	19	20	–	–	–	–	–	–	–	–	–	–	–	–
6	22	23	18	21	–	–	–	–	–	–	–	–	–	–	–	–
7	8	24	11	19	–	–	–	–	–	–	–	–	–	–	–	–
8	22	24	16	20	–	–	–	–	–	–	–	–	–	–	–	–

Table 5. Coherence of quantitative traits with seed color determined by differences between progeny seed color classes

Cross	No. of lines				Harvest index		Heading date		Height		Growth habit		Panicle length		Spikelets/ panicle	
	Light		Dark													
	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981
HMF																
1	24	26	15	16	C	–	C	C	C	C	C	–	–	–	–	–
2	22	22	23	24	–	–	–	–	–	–	–	–	–	–	–	–
3	27	32	7	11	–	–	–	–	–	–	–	–	–	–	–	–
4	14	15	26	29	C	–	C	–	–	–	C	–	–	–	–	–
LMF																
5	20	21	23	24	–	C	–	–	–	–	–	–	–	–	–	–
6	19	22	23	24	–	–	–	–	–	–	–	–	–	–	–	–
7	8	18	8	21	C	C	C	C	–	C	C	C	C	–	–	C
8	15	17	21	23	–	–	–	–	–	–	C	C	–	–	–	–

population for trait i. Since one parental species must be numerically greater for all characters when computing W or Y (Goodman 1966), certain variables were transformed for all genotypes as follows, making *A. fatua* phenotype numerically larger: 100 – harvest index, 10 – 100-seed weight, 100 – groat percentage, 25 – emergence.

Results and discussion

A. sativa/*A. fatua* hybrids had a mean MF of 0.96 with a variance of 0.38 (Table 3). MF ranged from 0.22 to 2.82 among *A. sativa*/*A. fatua* hybrids. McMullen et al. (1982) using the same nine *A. sativa* parents crossed with seven *A. sterilis* parents observed that *A. sativa*/*A. sterilis* hybrids had a mean MF of 1.17 and variance of 0.22. In their study MF ranged from 0.25 to 3.25. Thus, variation for MF, and presumably meiotic irregularity, was similar in both sets of hybrids. Micronuclei frequency in HMF crosses was almost ten times that in LMF crosses (Table 1).

'Noble', 'Jaycee' and 'MN67201' had the highest average MF crosses with *A. fatua* (Table 3) and *A. sterilis* (McMullen et al. 1982). These three *A. sativa* genotypes

Table 4 (continued)

Cross	Nodes/ panicle		Second leaf area		100-seed weight		Seeds/ panicle		Emergence	Groat percentage	Groat oil percentage	No. of coherent traits	
	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981	1981	1980	1981
HMF													
1	C	–	C	–	–	–	–	C	–	C	–	5	2
2	–	–	–	–	C	C	–	–	C	C	–	4	2
3	–	–	–	–	–	–	–	C	C	C	–	1	4
4	–	–	–	–	–	–	–	–	C	–	–	1	0
											Total	11	8
LMF													
5	–	–	–	–	–	–	–	–	C	–	–	1	0
6	–	–	–	–	–	–	–	–	C	–	–	1	0
7	–	–	–	–	–	–	–	–	C	C	–	1	1
8	–	–	–	–	–	–	–	–	C	C	–	1	1
											Total	4	2

C = character coherence between disarticulation habit and quantitative trait ($P \leqq 0.05$)

Table 5 (continued)

Cross	Nodes/ panicle		Second leaf area		100-seed weight		Seeds/ panicle		Emergence gence	Groat percentage	Groat oil percentage	No. of coherent traits	
	1980	1981	1980	1981	1980	1981	1980	1981	1980	1981	1981	1980	1981
HMF													
1	C	C	–	C	–	–	C	C	C	C	C	7	7
2	–	–	–	–	–	–	–	–	C	C	C	1	2
3	–	–	–	–	–	–	–	–	C	C	–	1	1
4	C	C	–	–	–	–	–	–	C	–	–	5	2
											Total	14	12
LMF													
5	–	–	–	–	–	–	–	–	C	C	–	1	2
6	–	–	–	–	–	–	–	–	C	–	–	1	0
7	C	–	C	–	C	–	–	–	C	C	–	8	6
8	–	–	–	–	–	–	–	–	C	C	C	2	3
											Total	12	11

C = character coherence between seed color and quantitative trait ($P \leqq 0.05$)

may differ from both wild species by common structural and/or genetic factors controlling chromosome pairing.

Estimates of variance for MF among crosses involving a given parent were frequently as high as the variance for MF among all crosses (Table 3). Thus MF in future crosses involving a specific parent would not be predicted well by the average MF in past crosses involving that parent. McMullen et al. (1982) also urged such caution.

Incidence of coherence of quantitative characters with seed disarticulation and color is shown in Tables 4 and 5, respectively. Character coherence is based on the difference between the means for quantitative traits of progeny lines displaying the seed morphology of the parental species (i.e. mean of nonshattering lines minus mean of shattering lines and mean of light-colored lines minus mean of dark-colored lines). Coherence was, in general, infrequently observed except for emergence and groat percentage.

A higher incidence of coherence would be expected in HMF crosses than in LMF crosses if higher MF is associated with decreased genetic recombination. This

Table 6. Coefficients of concordance (W, Y and Z)

Cross	Coefficients computed using characters:											
	1 through 10						1 through 11			1 through 10, 12, 13		
	W	Y	Z	W	Y	Z	W	Y	Z	W	Y	Z
HMF	1980			1981			1980			1981		
1	0.682	0.664	0.628	0.555	0.581	0.530	0.600	0.601	0.580	0.471	0.483	0.428
2	0.630	0.618	0.353	0.558	0.544	0.270	0.525	0.521	0.314	0.373	0.361	0.121
3	0.622	0.622	0.565	0.587	0.570	0.427	0.566	0.560	0.523	0.436	0.420	0.285
4	0.618	0.615	0.612	0.575	0.579	0.510	0.519	0.511	0.526	0.409	0.417	0.319
Mean	0.638	0.630	0.540	0.569	0.568	0.434	0.552	0.548	0.486	0.422	0.420	0.288
	±0.015	±0.011	±0.064	±0.008	±0.009	±0.059	±0.019	±0.020	±0.059	±0.021	±0.025	±0.064
LMF												
5	0.615	0.633	0.567	0.563	0.554	0.399	0.493	0.527	0.512	0.445	0.438	0.299
6	0.701	0.656	0.507	0.549	0.547	0.341	0.568	0.529	0.437	0.453	0.456	0.269
7	0.499	0.537	0.441	0.488	0.519	0.420	0.441	0.474	0.401	0.405	0.434	0.319
8	0.713	0.713	0.702	0.555	0.567	0.439	0.575	0.575	0.498	0.388	0.458	0.250
Mean	0.632	0.635	0.554	0.539	0.546	0.400	0.519	0.526	0.487	0.423	0.447	0.284
	±0.049	±0.037	±0.056	±0.017	±0.010	±0.021	±0.032	±0.021	±0.044	±0.015	±0.006	±0.015

W = Kendall's coefficient of concordance; Y = Goodman's multinormal coefficient of concordance; Z = Goodman's parental coefficient of concordance. See text for further explanation

pattern was apparent for seed disarticulation (Table 4), but not for seed color (Table 5). However, only certain crosses accounted for most of the coherence observed. Coherence with seed disarticulation was most frequent in crosses 1, 2, and 3, while coherence with seed color was most frequent in crosses 1, 4, and 7.

Estimates of recombination spindle width, the coefficients of concordance W, Y, and Z, are presented in Table 6. Values of W, Y, and Z can range from zero to one. Higher values (near one) indicate narrow spindle width and greater coherence of quantitative traits. All values of W in this study were greater than zero ($P < 0.01$, Gibbons 1971). The properties of non-null distributions of W, and the distributions of Y, and Z are not known. However, values of W, Y and Z for the eight crosses generally seemed to vary about a mean midway between zero and one. Therefore, the values were assumed to be independent, random samples from an approximately normal distribution and the sample variance was determined for each MF group.

HMF and LMF means for W, Y and Z (Table 6) were similar and standard errors were frequently overlapping for combinations of characters in both years. W, Y and Z were computed for additional subsets of characters (not shown) with the same results. Therefore, differences in coherence among these traits, as measured by W, Y and Z, did not correspond to differences in MF in these crosses.

Values of W, Y and Z that we observed were considerably larger than Goodman (1966) found for interspecific *Gossypium* crosses and backcrosses. He used characters that he believed were developmentally independent. Several of the characters we studied, such as heading date, height, the panicle traits, and second leaf area, are probably not developmentally independent. In addition, seeds per panicle is mathematically related to 100-seed weight and harvest index (Table 2). These relationships could increase correlations and, thus, partly account for the coherence among these characters.

W, Y and Z were lowered when emergence was added to the first ten variables in 1980 and when groat percentage and groat oil percentage were added in 1981. These characters were evidently less developmentally and/or genetically coherent with the first ten characters than the first ten characters were with one another.

Values of W and Y for each cross were similar to each other in our study indicating the general similarity of rank and product-moment correlations. Goodman (1966) found the same results. However, since Goodman used only one set of parents he could not observe how Z might vary with different pairs of parents. Z accounts for differences among crosses in the phenotypic similarity of their parents and in the phenotypic variation among progeny as well as correlations between characters. We found that Z varied more among crosses than did W or Y (Table 6). Crosses 2 and 6 tended to have relatively low values of Z while crosses 1, 4 and 8 had higher values. The parents of crosses 2 and 6 were phenotypically more similar for several characters than the parents of crosses 1, 4 and 8, but phenotypic variation among progeny lines was similar for all crosses (not shown). This tended to reduce a_i values (the weights for the correlations, see "Materials and

methods") and, thus, decrease Z values in crosses between more phenotypically similar parents (e.g. crosses 2 and 6).

Our results indicate that differences in MF among these *A. sativa*/*A. fatua* hybrids were not consistently related to coherence in their progenies of at least some of the traits which distinguish the parental species. There are several possible explanations for a lack of consistent relationship between MF and coherence in these oat crosses. Fu and Sears (1973), in studies with wheat, noted that chiasma failure and subsequent univalent formation at metaphase I do not necessarily indicate that crossing over has not occurred. If this situation exists in oats, then differences in MF among hybrids would not necessarily predict differences in genetic recombination or character coherence. McMullen et al. (1982) postulated structural differences – translocations and duplication-deficiencies – for relatively few chromosomes between *A. sativa* and *A. sterilis* lines. Structural differences are fairly frequent in hexaploid oats (Ladizinsky 1970) and, therefore, likely exist between certain *A. sativa* and *A. fatua* lines. As many as two to three micronuclei/quartet could be accounted for by asynapsis or desynapsis of just one or two chromosome pairs with structural differentiation. Recombination in the remaining 19 or 20 pairs could be essentially normal. In addition, random, independent assortment of 21 pairs provides for considerable whole-chromosome recombination that could reduce character coherence and diminish the effects of reduced homology in a few chromosome pairs in interspecific hybrids.

McMullen et al. (1982) found that pollen fertility and seed set were reduced in *A. sativa*/*A. sterilis* hybrids compared to the parents or intraspecific hybrids. Gametes (male or female) resulting from meioses with abnormal chromosome pairing are possibly selectively eliminated. If this were the case, then microspores with micronuclei may not become viable pollen. Not all quartets in our study or that of McMullen et al. (1982) contained micronuclei, even in crosses with high MF. Thus, if quartets without micronuclei had relatively normal meiosis and crossing over, and formed the majority of viable pollen, then MF would not necessarily reflect the recombination potential in male gametes. Likewise, differences in MF among hybrids would not necessarily indicate differences in meiotic irregularity or recombination in female gametes.

Our analyses gave information on character coherence and recombination but could not detect the degree of genetic recombination per se. Variation in micronuclei frequency among crosses would presumably reflect differing potential for genetic recombination in high and low MF crosses. This relationship was apparent in the coherence of quantitative traits with seed disarticulation but not with seed color.

Acknowledgements. Scientific Journal Series Paper No. 13,680 of the Minnesota Agricultural Experiment Station. Part of a thesis submitted by the senior author in partial fulfillment of the requirements for the PH.D. degree. The authors gratefully acknowledge M. S. McMullen for providing microsporocyte observations, the Quaker Oats Company for financial assistance and H. W. Rines, USDA-ARS, Research Geneticist, St. Paul, Minnesota for his encouragement and support.

References

Adkins SW, Ross JD (1981) Studies in wild oat seed dormancy. 1. The role of ethylene in dormancy breakage and germination of wild oat seeds (*Avena fatua* L.). Plant Physiol 67:358–362

Anderson E (1939) Recombination in species crosses. Genetics 24:668–698

Anderson E (1949) Introgressive hybridization. Wiley and Sons, New York

Burrows VD (1970) Yield and disease escape potential of fall-sown oats possessing seed dormancy. Can J Plant Sci 50: 371–377

Campbell AR, Frey KJ (1972) Association between groat protein percentage and certain plant and seed traits in interspecific oat crosses. Euphytica 21:352–363

Clausen J, Heisey WM (1960) The balance between coherence and variation in evolution. Proc Natl Acad Sci USA 46:494–506

Frey KJ (1976) Plant breeding in the seventies – useful genes from wild species. Egypt J Genet Cytol 5:460–482

Frey KJ (1977) Protein of oats. Z Pflanzenzücht 78:185–215

Frey KJ, Browning JA (1976a) Registration of 'Multiline M72' oat cultivar. Crop Sci 16:311

Frey KJ, Browning JA (1976b) Registration of 'Multiline E72', 'Multiline E73', and 'Multiline E74' oat cultivars. Crop Sci 16:311–312

Frey KJ, Hammond EG, Lawrence PK (1975) Inheritance of oil percentage in hexaploid oats. Crop Sci 15:94–95

Fu TK, Sears ER (1973) The relationship between chiasmata and crossing over in *Triticum aestivum.* Genetics 75: 231–246

Gibbons JD (1971) Nonparametric statistical inference. McGraw-Hill, New York

Goodman MM (1966) Correlation and structure of introgressive populations. Evolution 20:191–203

Ladizinsky G (1970) Chromosome rearrangements in the hexaploid oats. Heredity 25:457–461

Lyrene PM, Shands HL (1975) Associations among traits in progenies from *Avena sativa* L. × *A. sterilis* L. crosses. Crop Sci 15:361–363

McMullen MS, Phillips RL, Stuthman DD (1982) Meiotic irregularities in *Avena sativa* L./*A. sterilis* L. hybrids and breeding implications. Crop Sci 22:890–897

Rines HW, Stuthman DD, Briggle LW, Youngs VL, Jedlinski H, Smith DH, Webster JA, Rothman PG (1980) Collection and evaluation of *Avena fatua* L. for use in oat improvement. Crop Sci 20:63–68

Smith HH (1950) Developmental restrictions on recombination in *Nicotiana.* Evolution 4:202–211

Suneson CA (1967a) Registration of 'Rapida' oats. Crop Sci 7:168

Suneson CA (1967b) Registration of 'Sierra' oats. Crop Sci 7:168

Taylor JS, Simpson GM (1980) Endogenous hormones in after-ripening wild oat (*Avena fatua* L.) seed. Can J Bot 58:1016–1024