EFFECT OF THE NUMBER AND POSITION OF INTERCHANGES ON THE FERTILITY OF HYBRIDS INVOLVING NORMAL AND HOMOZYGOUS INTERCHANGE STOCKS OF BARLEY

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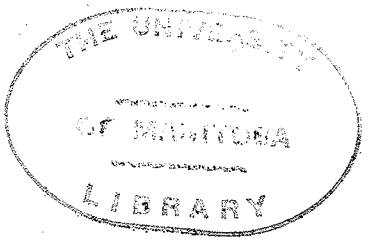

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ABSTRACT

Homozygous interchange stocks of barley were intercrossed, and also crossed with the normal stock Montcalm, to produce plants heterozygous for interchanges at different levels of chromosome participation. The fertility of interchange heterozygotes decreased as the number of chromosomes involved in interchanges increased. When the same level of interchange chromosome participation occurred, sterility was dependent on the size of the chromosome ring or rings formed at meiosis. Thus, plants with a ring of eight chromosomes had a higher sterility than plants with two rings of four chromosomes; plants with a ring of ten were more sterile than plants with a ring of six plus a ring of four; the sterility of plants with either two rings of six, or a ring of eight plus a ring of four, was higher than that of plants with three rings of four chromosomes.

Diallel crosses within both (a-b) and (c-f) interchange stocks were made. In six (a-b) interchange stocks, metaphase configurations of seven bivalents were observed in the F_1's from crosses made

among C1343, C1384, C1385, XT8, and Ert7. Both a ring of four configuration and seven bivalents were found in the F_1's from crosses made between these stocks and XT12. In the seven (c-f) interchange stocks, plants from crosses among XT10, Ert1, Ert14, and XT6 as well as crosses among XT4, Ert47, and C1336 formed seven bivalents at meiosis, while crosses between these two groups gave rise to plants in which both ring of four configurations and seven bivalents were observed. A similar degree of sterility was found in plants with and without ring formation.

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INTRODUCTION

The "Oenothera" method of establishing homozygous lines from promising hybrids, has been suggested for species which have a relatively low number of chromosomes and where a relatively high degree of fertility can be maintained in plants heterozygous for interchanges (5).

To date, the incorporation of appropriate interchanges in a single stock, which if crossed with a normal stock would produce a complete ring of all chromosomes, has not been achieved. Barley (Hordeum spp.) would appear to be an excellent experimental crop to test the "Oenothera" method of establishing homozygous lines because of the relatively low chromosome number and because at the single interchange level the fertility of interchange heterozygotes appears to be fairly high.

Final synthesis of a stock homozygous for interchanges involving all 14 chromosomes, that will be useful in testing the "Oenothera" method, will depend on the position of interchanges in the stock and the degree of sterility of the heterozygotes produced when it is crossed with normal stocks.

Since very little is known about the fertility of various complex interchange combinations, and how fertility may be affected by the position of interchanges, these phenomena are worthy of study.

A collection of a large number of interchange stocks

of barley has been made, and by suitable crossings, it should be possible to build up complex interchanges heterozygotes. For the stocks that involve interchange between the same two pairs of chromosomes, it should be possible to study the positions of the breakage points and how these may affect fertility.

The objectives of this study were designed therefore to investigate:

(1) The fertility of interchange heterozygotes at different levels of chromosome participation.

(2) The effect of the relative positions of the points of interchange on metaphase pairing and fertility in the F_1's resulting from diallel crossing within different (a-b)* and (c-f) stocks.

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* The seven chromosomes of barley have been assigned the letters a to g by Burnham et al. (10). The hyphenated letters indicate the interchange chromosomes involved in homozygous interchange stocks.

LITERATURE REVIEW

Interchanges are the result of exchanges of segments between non-homologous chromosomes. They were first termed "segmental chromosomal interchanges", but are now more simply referred to as interchanges, reciprocal translocations, or translocations (8). The interchanges may arise "spontaneously", may be induced by irradiation or may be produced by treatment with certain chemicals.

According to Burnham (8), the first observation of more than two chromosomes attached, so as to form a ring at meiosis, was reported by Gates in Oenothera rubinervis L. The first account of the breeding behavior of a probable case of interchanged chromosomes was reported by Belling (2). He proposed a two-gene hypothesis to account for the 50 per cent aborted pollen in the F_1 of a velvet bean cross, but he also pointed out that the abnormal behavior of two chromosome pairs may explain the results. That interchanges were responsible was not interpreted until 1925, when he explained this breeding behavior on the basis of "segmental interchange between non-homologues" (3). Since then, the phenomenon of interchanges has been widely studied in a number of plants.

Belling's explanation of chromosomal ring formation at the time of reduction division (4), has been applied to

explain ring formations in Oenothera and other genera (13, 14, 15). After Burnham's proposal that the "Oenothera" method may be applied to gamete selection (5), attempts have been made to build a large ring in maize (Zea mays L.), Einkorn wheat (Triticum monococcum L.) and barley, by a series of crosses between, or by cyclic irradiation of, existing interchange stocks. A ring of 10 chromosomes (@10) in maize was obtained from cyclic irradiation of an interchange stock (8). This was obtained in successive steps. First, a ring of eight chromosomes (@8) was produced by X-irradiation of a stock homozygous for one interchange. Then a stock homozygous for the interchanges involving the four pairs of chromosomes was X-rayed to produce lines which differed from it by one additional interchange. Yamashita (45) developed a ring of 14 chromosomes in T. monococcum L., but both parents of the cross contributed interchanges. Nishimura et al. (34) and Nishimura and Kurakami (33) suggested that a stock in barley which will give a ring of eight plus a ring of six (@8+@6) or a ring of 10 plus a ring of four (@10+@4) in crosses may be synthesized in a shorter time then a complete ring of 14 chromosomes.

When a normal stock is crossed with a stock involving one interchange, three possible types of chromosome pairing may occur at meiosis in the F_1 (8). The interchanged chromosomes are usually associated in a ring, if the exchanged segments are long. They appear as a chain if one long segment

has exchanged with a very short one. When both segments are short, either chains or two bivalents will be formed. The last type of chromosome pairing has been reported by Clarke and Anderson (12) in maize.

Chromosome pairing at meiotic metaphase in the F_1 plants obtained by intercrossing two stocks involving interchanges between the same two pairs of chromosomes, has been reported by Hagberg (22) and Turcotte (43). Working with barley, Hagberg (22) observed seven bivalents in the F_1 of Tr_7 and Tr_{ab}, both involving the (a-b) interchange. He doubted that the breakage points would be at the same position in both stocks, and consequently suspected that pairing of non-homologous segments must have occurred. In maize, Turcotte (43) studied the chromosome behavior in the F_1's of three crosses, T1-9a x T1-9c, T2-6c x T2-6d, and T3-7a x T3-7b. Within each cross, the parental stocks involved interchanges between the same two chromosomes but the breakage points were at different positions. Diakinesis in all F_1's showed 10 bivalents. Some of the cells from the cross T3-7a x T3-7b had a bivalent with homologues of unequal length. Pachytene analysis for T1-9a x T1-9c showed intercalary loops in both chromosomes 1^9 and 9^1. For T3-7a x T3-7b T-shaped configurations were observed for both chromosomes 3^7 and 7^3 at pachytene. No loops in either chromosome 2^6 or 6^2 of the cross T2-6c x T2-6d were observed at pachytene, and the average pollen abortion of the F_1 plants

was 7.3 per cent. These results suggested that the breakage points of T2-6c and T2-6d were identical or nearly so, in disagreement with published breakage positions of these two interchanges (7).

It is generally assumed that zigzag rings or chains lead to alternate separation of the associated chromosomes. These will eventually develop into normal gametes. Adjacent separation produces abortive gametes with chromosomal deficiency-duplication. Burnham (8) reported that as a result of the nearly equal frequency of alternate and adjacent separation of chrmmosomes at anaphase I in species such as Zea mays L., Pisum sativum L., Sorghum versicolor Andersa. and Petunia spp., pollen and ovule abortions are usually about 50 per cent. In a number of other species such as Oenothera spp., Triticum monococcum L., T. durum Desf. and probably barley and Datura spp., in which from 70 to 90 per cent alternate separation at reduction division is characteristic, abortion usually is much lower. However, in a species with predominant alternate separation, the degree of sterility depends on the amount of crossing-over which occurs in the interstitial segments. It could approach 50 per cent if those regions were long (6, 7).

In barley, the first reported interchange was by Smith (39). Since then many references to interchanges in barley appeared (8, 9, 22, 23, 25, 32, 33, 34, 35, 40, 44). In order to identify chromosomes involved in inter-

change, Burnham and Hagberg (9) and Burnham et al. (10), using a number of interchange stocks developed at the Minnesota Agricultural Experiment Station and at Svalöf, established a tester set of interchange stocks.

The fertility of interchange homozygotes is not affected as indicated by Nybom (35), who reported that yielding ability was not greatly disturbed in the 19 homozygous interchange stocks of barley he studied. Various degrees of sterility have been reported in interchange heterozygotes, most of the reports dealing with relatively simple interchanges. The published information on sterility has been summarized and appears in Table 1.

TABLE 1. Sterility of interchange heterozygotes in barley.

Number and size of ring	Sterility per cent		Pollen abortion per cent		Number evaluated		Authority
	Average	Range	Average	Range	Lines	Plants	
04	-	20.6- 92.2	28.8	14.4-58.0	34	-	(10)
"	23	-	-	-	10	-	(23)
"	-	48.7- 77.4	-	-	-	3	(32)
"	35.5	25.5- 48.5	19.9	15.1-28.0	16	73	(34)
"	-	31.0- 35.2	-	-	2	3	(39)
"	28	-	28	-	-	-	(41)
"	-	10 - 50	-	-	6	-	(44)
06	-	54 - 58	-	-	2	10	(33)

(Continued next page)

TABLE 1. (Continued)

Number and size of ring	Sterility per cent		Pollen abortion per cent		Number evaluated		Authority
	Average	Range	Average	Range	Lines	Plants	
06	-	46.8- 52.5	32.7	-	2*	9	(34)
204	67	-	51	-	1	-	(10)
"	-	48.7- 88.7	-	-	-	4	(32)
"	-	52 - 55	-	-	3	23	(33)
"	52	-	-	-	1	2	(34)
08	-	71.3-100.0	-	-	-	4	(32)
"	-	70 - 74	-	-	2	19	(33)
06+04	-	41.7- 77.5	-	-	-	9	(32)
"	71	-	-	-	1	4	(33)
304	-	50.0- 73.7	-	-	-	6	(32)
08+04	-	61.0-100.0	-	-	-	18	(32)
012	-	90.7-100.0	-	-	-	3	(32)
08+204	-	73.0- 92.4	-	-	-	6	(32)
08+06	-	92.9-100.0	-	-	-	2	(32)
010+04	-	87.5-100.0	-	-	-	6	(32)

* Value of pollen abortion was evaluated from one line only.

Chromosome breaks may be induced by chemical treatment or by irradiation. The hypothesis that some chemicals cause chromosome breakage selectively in heterochromatin, as proposed by Ford (17), has been studied and confirmed (16, 19, 27, 29). Alternatively, there are different opinions whether or not irradiation causes preferential breakages of chromosomes.

Patterson et al. (35) found that the majority of X-ray induced breaks in Drosophila chromosomes occurred at either the free or spindle fiber ends. But according to Bauer et al. (1), X-irradiation of the X-chromosomes of Drosophila resulted in a more or less random distribution of breaks, but still with a significantly higher frequency of breakage in the heterochromatic proximal portion. Kaufmann (25, 26), in a more extensive study in Drosophila, found that breaks were distributed at random along the chromosomes except for the proximal heterochromatic regions and for similar intercalary regions. In the grasshopper, the highest frequency of breaks occurred near the spindle attachment (24).

In Tradescantia microspores, both spontaneous (18) and X-ray induced (18, 38) breaks tended to be most frequent at the proximal regions. According to Sax (37), an excess of X-ray induced breaks in the proximal region of the chromosome arms has also been observed in Crepis by Lewitsky and Sizova. Camara et al. (10) reported that breakage and reunion of chromosomes,

as induced by X-rays, occurred near or at the centromere in Triticum. Swanson (42), working with Tradescantia, found that treatment of the generative nucleus in the pollen tube, either with ultraviolet or X-rays, produced a higher frequency of deletions in the medial and distal arms. Graf (19), however, has reported that the frequency of X-ray induced breakages was independent of the knob number in maize, indicating no preferential breakage of X-rays in heterochromatin.

Burnham and Hagberg (9), working with barley, reported a higher frequency of X-ray induced breaks in the "b" chromosome than in any other chromosome. No other reports dealing with preferential breakages of barley chromosomes have been noted.

MATERIALS AND METHODS

The experiments involved in this study were conducted in 1958 and 1959. Forty-seven homozygous interchange stocks of barley and two normal stocks were used. The two normal stocks (varieties Herta and Montcalm) served as checks in the study of sterility. In addition, Montcalm was used as a parent stock in many of the crosses. The interchange stocks were selected from the interchange stock collection of the Department of Plant Science, at the University of Manitoba. The interchange stocks, their origin, and the chromosomes involved in the interchanges are listed in the Appendix.

During the summer of 1958 and the spring of 1959 a total of 112 crosses was made. Of these, 76 crosses were either between various interchange stocks or between Montcalm and interchange stocks. The remaining 36 crosses were the diallel combinations within the (a-b) and (c-f) interchange stocks. The 76 "inter" crosses and the expected configurations at meiotic metaphase are presented in Table 2. The 36 "intra" crosses are presented in Table 3.

From each cross made in the summer of 1958 a maximum of 10 F_1 plants was grown under greenhouse conditions in the fall at a spacing of 4 by 7 inches. In the summer of 1959, all seeds from crosses made in the spring, and also remnant seeds from some of the 1958 crosses, were grown in the field at a spacing of 4 inches apart within rows and 1 foot apart between rows. Herta and Montcalm, used as checks,

TABLE 2. Crosses involving interchange stocks and with Montcalm, and the expected metaphase configuration in the F_1 plants.

Cross and interchange chromosomes involved			Expected configuration in F_1	
			Number and size of ring	Chromosomes involved
Montcalm	x	C1384(a-b)	04	a-b
Montcalm	x	C1385(a-b)*	"	"
XT8(a-b)	x	Montcalm	"	"
Montcalm	x	XT12(a-b)	"	"
Ert7(a-b)	x	Montcalm	"	"
Montcalm	x	C1343(a-b)	"	"
C1336(c-f)	x	Montcalm	"	c-f
Montcalm	x	XT10(c-f)*	"	"
Ert14(c-f)	x	Montcalm	"	"
Ert47(c-f)	x	Montcalm	"	"
Montcalm	x	XT4(c-f)*	"	"
Montcalm	x	XT16(a-e)	"	a-e
C1456(a-e)	x	Montcalm	"	"
Montcalm	x	C1025(b-d)	"	b-d
Montcalm	x	XT2(d-g)*	"	d-g
C1365(b-c)	x	Montcalm	"	b-c
C1310(b-f)	x	Montcalm	"	b-f
C1483(b-g)	x	Montcalm	"	b-g
C1432(c-e)	x	Montcalm	"	c-e
XT11(a-c)	x	XT8(a-b)	06	a-b-c
XT18(a-f)	x	XT9(a-g)	"	a-f-g
C1025(b-d)	x	C1483(b-g)	"	b-d-g

* Includes reciprocal cross

(Continued next page)

TABLE 2. (Continued)

Cross and interchange chromosomes involved			Expected configuration in F_1	
			Number and size of ring	Chromosomes involved
7031(a-d)	x	C1405(c-d)	06	a-c-d
Montcalm	x	4256-1(a-c-d)	"	"
XT2(d-g)	x	C1420(e-f)*	204	(d-g)(e-f)
XT12(a-b)	x	C1340(c-d)	"	(a-b)(c-d)
XT6(c-f)	x	XT12(a-b)	"	(a-b)(c-f)
XT18(a-f)	x	C1483(b-g)*	"	(a-f)(b-g)
II-4(a-f)(b-g)	x	Montcalm	"	"
III-15(d-g)(c-e)	x	Montcalm	"	(d-g)(c-e)
VII-9(a-f)(c-e)	x	Montcalm	"	(a-f)(c-e)
XVII-2(a-b)(e-f)	x	Montcalm	"	(a-b)(e-f)
XXXIX-14(b-d)(c-f)	x	Montcalm	"	(b-d)(c-f)
C1385(b-d)	x	4256-1(a-c-d)	08	a-b-c-d
XT8(a-b)	x	4256-1(a-c-d)	"	"
C1336(c-f)	x	4256-1(a-c-d)	"	a-c-d-f
XT4(c-f)	x	4256-1(a-c-d)	"	"
XT10(c-f)	x	4256-1(a-c-d)	"	"
C1483(b-g)	x	4256-1(a-c-d)	06+04	(a-c-d)(b-g)
C1482(e-f)	x	4256-1(a-c-d)	"	(a-c-d)(e-f)
C1420(e-f)	x	4256-1(a-c-d)	"	"
C1346(b-e)	x	4256-1(a-c-d)	"	(a-c-d)(b-e)
VII-9(a-f)(c-e)	x	4256-1(a-c-d)	010	a-c-d-e-f
III-15(d-g)(c-e)	x	4256-1(a-c-d)	"	"
II-4(a-f)(b-g)	x	XVII-2(a-b)(e-f)	"	a-b-e-f-g
XVII-2(a-b)(e-f)	x	VII-9(a-f)(c-e)	"	a-b-c-e-f

* Includes reciprocal cross

(Continued next page)

TABLE 2. (Continued)

Cross and interchange chromosomes involved			Expected configuration in F_1	
			Number and size of ring	Chromosomes involved
XT2(d-g)	x	VII-9(a-f)(c-e)*	3Ø4	(a-f)(c-e)(d-g)
XTL(c-g)	x	XVII-2(a-b)(e-f)*	"	(a-b)(e-f)(c-g)
XT12(a-b)	x	III-15(c-e)(d-g)*	"	(a-b)(c-e)(d-g)
II-4(a-f)(b-g)	x	4256-1(a-c-d)	08+04	(a-c-d-f)(b-g)
XVII-2(a-b)(e-f)	x	4256-1(a-c-d)	"	(a-b-c-d)(e-f)
II-4(a-f)(b-g)	x	XXXIX-14(b-d)(c-f)	206	(a-c-f)(b-d-g)
III-15(c-e)(d-g)	x	XXXIX-14(b-d)(c-f)	"	(b-d-g)(c-e-f)
XVII-2(a-b)(e-f)	x	XXXIX-14(b-d)(c-f)	"	(a-b-d)(c-e-f)
III-22(c-e)(d-g)	x	XVII-2(a-b)(e-f)	06+204	(c-e-f)(a-b)(d-g)
III-15(c-e)(d-g)	x	XVII-2(a-b)(e-f)	"	"
III-15(c-e)(d-g)	x	II-4(a-f)(b-g)	"	(b-d-g)(a-f)(c-e)

* Includes reciprocal cross

were grown as border rows in 1958, and at every tenth row in 1959. Parental stocks were also grown in 1959.

Pollen mother cells from the second or third tillers of F_1 plants were examined cytologically in both years, using the acetocarmine smear technique described by Smith (40).

Seed set was determined for each F_1 plant. In 1958, one spike from every F_1 plant was used for seed counts. In 1959, more than one spike from each plant was evaluated. Per cent sterility

TABLE 3. Diallel crosses within the (a-b) and (c-f) interchange stocks.

Crosses within (a-b) interchange stocks					
C1343	x	C1384	C1384	x	XT12
C1343	x	C1385	C1385	x	XT8
C1343	x	XT8	C1385	x	Ert7
C1343	x	Ert7	C1385	x	XT12
C1343	x	XT12	XT8	x	Ert7
C1384	x	C1385	XT8	x	XT12
C1384	x	XT8	Ert7	x	XT12
C1384	x	Ert7		-	

Crosses within (c-f) interchange stocks					
XT10	x	Ert1	Ert14	x	XT6
XT10	x	Ert14	Ert14	x	C1336
XT10	x	XT6	Ert14	x	Ert47
XT10	x	C1336	Ert14	x	XT4
XT10	x	Ert47	XT6	x	C1336
XT10	x	XT4	XT6	x	Ert47
Ert1	x	Ert14	XT6	x	XT4
Ert1	x	XT6	C1336	x	Ert47
Ert1	x	C1336	C1336	x	XT4
Ert1	x	Ert47	Ert47	x	XT4
Ert1	x	XT4		-	

was determined by:

$$\frac{\text{number of sterile spikelets}}{\text{total number of spikelets}} \times 100.$$

In six-rowed spikes, seed counts were made on the two center rows in 1958. The count was extended to the lateral rows as well in 1959 in order to obtain larger size samples.

In the fall of 1958 the hybrids grown in the greenhouse did not flower at the same time. A few had to be discarded because of the high degree of sterility which occurred presumably because of unfavorable growing conditions at the time of flowering. During that period the greenhouse was covered by ice and the temperature in the greenhouse occasionally dropped to as low as 40°F. In the field experiment in 1959, severe damage to the hybrids and parents was caused by cutworms at the time of emergence. Before the cutworm damage was noticed and the cutworms controlled by the use of dieldrin, approximately three quarters of the nursery was destroyed.

RESULTS AND DISCUSSION

I. Crosses between Interchange Stocks and with Montcalm

(1) Cytological analysis

The number of plants examined and the configurations observed for each cross are shown in Table 4. The expected configurations were obtained in all but five crosses, these being XVII-2 x III-22, II-4 x XVII-2, XVII-2 x VII-9, XT1 x XVII-2, and III-15 x 4256-1. A total of seven parental stocks were involved in these crosses. Since six of these stocks were used in a number of crosses, it should be possible to trace the "suspect" parent or parents responsible for discrepancies.

The multiple-interchange stock XVII-2 was the common parent of four of the five problem crosses. Of the two plants of the cross XVII-2 x III-22 examined, the metaphase configuration was found to be the expected 06+204 in one plant, and 304 in the other. A 08 and the expected 010 were found in different F_1 plants of II-4 x XVII-2. In the cross XVII-2 x VII-9, the only F_1 plant studied cytologically was observed to form 06+04 instead of the expected 010. In XT1 x XVII-2, one plant gave rise to the expected 304, while a configuration of 06+04 was found in five other plants.

XT1 had only one interchange, and II-4 and VII-9 behaved as expected in other crosses in which they were involved. It is therefore unlikely that they were responsible for the discrepancies found in their respective crosses. To interpret

TABLE 4. Observed metaphase configuration and sterility in the F_1 plants of crosses involving interchange stocks and Montcalm.

Cross	No. of plants examined: Cytologically	No. of plants examined: For sterility*	Observed metaphase configuration	Sterility per cent: Average	Sterility per cent: Range
Expected configuration: 04					
Montcalm x C1384	2	7 (7)	04	43.6	35.7 - 51.8
Montcalm x C1385	1	2(10)	"	50.2	41.6 - 69.1
XT8 x Montcalm	1	10(14)	"	54.6	40.8 - 74.1
Montcalm x XT12	3	3 (3)	"	46.1	38.4 - 56.0
Ert7 x Montcalm	6	14(30)	"	52.8	39.5 - 68.8
Montcalm x C1343	1	2(10)	"	42.2	37.1 - 47.7
C1336 x Montcalm	2	9(10)	"	49.6	40.2 - 67.2
Montcalm x XT10	2	8(12)	"	47.1	41.0 - 54.1
Ert14 x Montcalm	2	10(19)	"	49.7	38.1 - 59.3
Ert47 x Montcalm	4	7 (7)	"	38.7	30.3 - 45.9
Montcalm x XT4	1	8 (8)	"	41.5	38.0 - 51.7
Montcalm x XT16	1	8 (8)	"	61.5	58.0 - 70.1
Montcalm x C1025	2	6 (6)	"	45.5	38.9 - 54.2
Montcalm x XT2	3	8 (8)	"	55.0	45.4 - 63.2
C1456 x Montcalm	1	1 (5)	"	26.4	-
C1365 x Montcalm	2	3(12)	"	37.3	29.9 - 45.2
C1310 x Montcalm	1	1 (5)	"	45.3	-
C1483 x Montcalm	3	4(20)	"	39.5	33.3 - 45.7
C1432 x Montcalm	1	1 (4)	"	34.3	-

* Figures in parentheses indicate number of spikes examined

(Continued next page)

TABLE 4. (Continued)

Cross	No. of plants examined: Cytologically	No. of plants examined: For sterility*	Observed metaphase configuration	Sterility per cent: Average	Sterility per cent: Range
Expected configuration: 96					
XT11 x XT8	2	4 (9)	96	84.2	76.3 - 85.9
XT18 x XT9	4	2 (8)	"	76.6	72.6 - 84.4
C1025 x C1483	3	7(15)	"	70.6	59.3 - 84.6
7031 x C1405	1	6 (6)	"	83.0	75.5 - 88.1
Montcalm x 4256-1	4	12(20)	"	62.2	50.0 - 72.1
Expected configuration: 204					
XT2 x C1420	6	9(16)	204	57.4	52.8 - 62.4
XT12 x C1340	4	7(11)	"	48.9	44.1 - 56.3
XT18 x C1483	1	4 (4)	"	52.5	49.4 - 56.8
XT6 x XT12	3	4(12)	"	71.9	59.7 - 83.7
II-4 x Montcalm	2	5(20)	"	70.5	58.9 - 82.7
III-15 x Montcalm	5	10(46)	"	58.0	54.9 - 66.5
VII-9 x Montcalm	1	1 (3)	"	84.4	-
XVII-2 x Montcalm	2	4(18)	"	78.3	72.8 - 85.9
XXXIX-14 x Montcalm	3	4 (7)	"	76.3	70.5 - 80.8
Expected configuration: 98					
C1358 x 4256-1	2	1 (1)	98	85.7	-
XT8 x 4256-1	2	3(11)	"	70.2	62.7 - 84.3
C1336 x 4256-1	1	3 (3)	"	76.4	69.9 - 81.7

* Figures in parentheses indicate number of spikes examined

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TABLE 4. (Continued)

Cross		No. of plants examined: Cytologically	No. of plants examined: For sterility*	Observed metaphase configuration	Sterility per cent: Average	Sterility per cent: Range
Expected configuration: 08 (Continued)						
XT4	x 4256-1	3	3 (4)	08	77.5	72.2 - 82.5
XT10	x 4256-1	1	1 (3)	"	83.6	-
Expected configuration: 06+04						
C1482	x 4256-1	2	3 (3)	06+04	81.6	74.4 - 85.2
C1483	x 4256-1	6	13(39)	"	80.4	73.8 - 88.2
C1346	x 4256-1	7	8(16)	"	83.3	71.8 - 89.8
C1420	x 4256-1	2	8(31)	"	72.1	68.1 - 83.0
Expected configuration: 010						
VII-9	x 4256-1	2	6(15)	010	87.9	83.3 - 93.5
III-15	x 4256-1	1	1 (2)	"	85.0	-
III-15	x 4256-1	1	1 (4)	06+04	86.3	-
II-4	x XVII-2	1	1 (8)	010	83.3	-
II-4	x XVII-2	1	-	08	-	-
XVII-2	x VII-9	1	1 (3)	06+04	93.0	-
Expected configuration: 304						
XT2	x VII-9	4	7 (7)	304	77.7	68.3 - 84.6
XT1	x XVII-2	1	1 (1)	"	75.0	-
XT1	x XVII-2	5	5(26)	06+04	87.5	77.9 - 92.7
XT12	x III-15	2	2 (8)	304	90.0	89.7 - 90.2

* Figures in parentheses indicate number of spikes examined

(Continued next page)

TABLE 4. (Continued)

Cross		No. of plants examined: Cytologically	No. of plants examined: For sterility*	Observed metaphase configuration	Sterility per cent: Average	Sterility per cent: Range
Expected configuration: 08+04						
II-4	x 4256-1	2	5(16)	08+04	89.2	85.3 - 92.8
XVII-2	x 4256-1	2	7(19)	"	93.1	86.6 - 96.3
Expected configuration: 206						
II-4	x XXXIX-14	1	3(19)	206	91.2	87.1 - 93.4
III-15	x XXXIX-14	1	1 (3)	"	95.6	-
XVII-2	x XXXIX-14	2	5(17)	"	92.1	87.5 -100.0
Expected configuration: 06+204						
III-22	x XVII-2	1	1 (1)	06+204	94.2	-
III-22	x XVII-2	1	1 (1)	304	87.6	-
III-15	x XVII-2	2	4(16)	06+204	96.9	95.2 - 97.9
III-15	x II-4	1	2(12)	"	99.1	98.4 - 99.8

* Figures in parentheses indicate number of spikes examined

the discrepancies described above, it was assumed that the XVII-2 parent was either heterozygous for the (a-b) interchange or was composed of two different types, i.e., (a-b)(e-f) and (a-b).

The four critical crosses were reassigned on the assumption that the (e-f) interchange was missing and the results presented in Table 5.

TABLE 5. The "expected" and observed metaphase configuration in the four F_1's involving XVII-2, assuming the absence of the (e-f) interchange in the XVII-2 gametes.

Cross			Chromosomes involved	Metaphase configuration	
				Expected	Observed
II-4 (a-f)(b-g)	x	XVII-2 (a-b)	a-b-f-g	0%	0%
XVII-2 (a-b)	x	VII-9 (a-f)(c-e)	(a-b-f)(c-e)	96+4	96+4
XT1 (c-g)	x	XVII-2 (a-b)	(a-b)(c-g)	2%	96+4
III-22 (d-g)(e-e)	x	XVII-2 (a-b)	(a-b)(d-g)(e-e)	3%	3%

As can be seen from Table 5, the "expected" configuration was obtained in three of the four crosses. Therefore it can be concluded that the XVII-2 stock is not homogeneous and should be purified. Further evidence will be presented in the section on sterility.

In the two remaining crosses, the discrepancies between observed and expected configurations are assumed to have been caused by the introduction of foreign pollen at the time of crossing or by some other error in handling.

(2) Sterility

In the greenhouse experiment in 1958, spikes of Herta and Montcalm were fully fertile except for those that headed during the period of unfavorable growing conditions (see

Materials and Methods).

In the field experiment in 1959, spikes of Herta, Montcalm and all parental stocks were carefully examined at harvest. About five per cent sterility was found in the parental stocks C1343, C1384, and C1385. Stock XVII-2 was estimated to have a sterility of 44.3 per cent (on the basis of counts made on 30 spikes) which would suggest that it is heterozygous for one interchange. All other parental stocks and the check varieties were fully fertile.

The variation in the sterility of hybrids at any one interchange level between years was no greater than within years and therefore the data on sterility for both years was combined and included with the cytological information presented in Table 4.

The range in average per cent sterility of the 19 crosses which had a 04 configuration at metaphase was from 26.4 to 61.5 per cent. The variation in per cent sterility from plant to plant within most of the crosses was greater than the variations between crosses. However, in the cross Montcalm x XT16 which had the highest per cent sterility, the lowest reading was higher than many of the highest readings obtained in other crosses. This would suggest that some of the interchanges in the heterozygous condition may have a greater effect on sterility than others. Further evidence that would support this hypothesis may be seen in the crosses at other interchange levels. In the 06 group,

the cross Montcalm x 4256-1 had by far the lowest per cent sterility and in this cross the most sterile plant was more fertile than the plants with the lowest sterility in three of the four remaining crosses. Similarly in the group which had the 204 configuration, the crosses XVII-2 x Montcalm and XXXIX-14 x Montcalm had a higher per cent sterility than the least fertile plants of four of the other crosses.

For each interchange level, i.e., 04, 06, etc., the data for all crosses were combined and are presented in Table 6.

In general, the sterility increased as the number of chromosomes involved in interchanges increased. For plants with the same number of interchanged chromosomes, those which formed a bigger ring or rings had a higher per cent sterility. Thus, 08 plants had a higher sterility than 204 plants; plants with 010 were more sterile than plants with 06+04; the sterility of 304 plants was lower than that of plants with either 08+04 or 206. This is in agreement with the results obtained by other workers (Table 1).

It should be noted that in the F_1 of the cross III-22 x XVII-2, a sterility of 94.2 per cent was found in a plant with the expected configuration of 06+204, while the sterility of another plant of the same cross, showing the unexpected configuration 304, was 87.6 per cent (see Table 4). This falls in the range of per cent sterility of plants with 304 (see Table 6).

TABLE 6. Sterility of interchange heterozygotes at different levels of interchanged chromosome participation.*

Number and size of ring	Number of crosses examined	Number of plants examined**	Sterility per cent	
			Average	Range
Ø4	19	112(198)	45.3	26.4 - 61.5
Ø6	5	31 (58)	75.3	62.2 - 84.2
2Ø4	9	48(137)	66.6	48.9 - 84.4
Ø8	5	11 (22)	78.7	70.2 - 85.7
Ø6+Ø4	4	32(109)	79.4	72.1 - 83.3
Ø10	3	8 (25)	85.4	83.3 - 87.9
3Ø4	3	10 (16)	80.9	75.0 - 90.0
Ø8+Ø4	2	12 (35)	91.2	89.2 - 93.1
2Ø6	3	9 (39)	93.0	91.2 - 95.6
Ø6+2Ø4	3	7 (29)	96.7	94.2 - 99.1

* Sterility of plants with unexpected metaphase configurations was not included.

** The figures in parentheses are the numbers of spikes examined.

II. Diallel Crosses within Interchange Stocks

(1) Diallel crosses within (a-b) interchange stocks

The results of the cytological and sterility studies of the F_1's from diallel crosses within six (a-b) interchange stocks are presented in Table 7.

TABLE 7. Metaphase configuration and sterility in the F_1 of diallel crosses within (a-b) interchange stocks.*

Cross	No. of plants examined: Cytologically	No. of plants examined: For sterility	Metaphase configuration	Sterility per cent
C1384 x XT12	4	4	04+5II	47.0
C1385 x XT12	2	6	04+5II	32.5
XT8 x XT12	2	2	04+5II	75.0
Ert7 x XT12	1	1	04+5II	38.5
Average of F_1 plants with 04+5II				48.3
C1343 x C1385	1	1	7II	41.8
C1343 x Ert7	3	7	7II	53.3
C1384 x XT8	4	6	7II	42.3
C1384 x Ert7	3	4	7II	46.4
C1385 x XT8	3	6	7II	50.4
C1385 x Ert7	1	5	7II	39.7
XT8 x Ert7	3	5	7II	67.3
Average of F_1 plants with 7II				48.8
Average				48.6

* Four of the diallel crosses were lost due to cutworm damage.

In the four crosses where XT12 was a common parent, configurations of both 04+5II and seven bivalents were found in the same plants. No ring formations were observed in the F_1 plants from seven crosses made between stocks other than XT12.

In Table 7 the crosses were grouped according to their

metaphase configurations, and the average per cent sterility of each group was calculated. The sterility of the four crosses involving ring formation ranged from 32.5 to 75.0 per cent, averaging 48.3 per cent. The average sterility of the seven crosses with seven bivalents was 48.8 per cent, with a range of 39.7 to 67.3 per cent. The weighted average of the two groups was 48.6 per cent.

(2) Diallel crosses within (c-f) interchange stocks

Results obtained in diallel crosses within the seven (c-f) interchange stocks were similar to those described above. They are presented in Table 8.

Metaphase configurations of 19 crosses were identified successfully. The results indicate that, if the interchange stocks were divided into two groups, one including XT10, Ert1, Ert14, and XT6, and the other XT4, Ert47, and C1336, plants from crosses within each group formed seven bivalents at meiosis, while crosses between groups gave rise to plants in which both ring of four configurations and seven bivalents were observed.

The average sterility was 49.4 per cent for the 12 crosses with ring formation at meiosis, and 52.8 per cent for the seven crosses with no ring formation, the range being 32.4 to 79.2 per cent and 27.8 to 65.0 per cent, respectively. The weighted average sterility of groups was 50.6 per cent.

TABLE 8. Metaphase configuration and sterility in the F_1 of diallel crosses within (c-f) interchange stocks.*

Cross	No. of plants examined: Cytologically	No. of plants examined: For sterility	Metaphase configuration	Sterility per cent
XT10 x C1336	4	6	Ø4+5II	42.9
XT10 x Ert47	1	1	Ø4+5II	57.4
XT10 x XT4	4	4	Ø4+5II	52.8
Ert1 x C1336	3	3	Ø4+5II	41.5
Ert1 x Ert47	3	7	Ø4+5II	41.9
Ert1 x XT4	2	3	Ø4+5II	43.8
Ert14 x C1336	2	2	Ø4+5II	35.7
Ert14 x Ert47	1	3	Ø4+5II	44.8
Ert14 x XT4	4	5	Ø4+5II	32.4
XT6 x C1336	5	5	Ø4+5II	44.9
XT6 x Ert47	1	1	Ø4+5II	79.2
XT6 x XT4	3	4	Ø4+5II	75.0
Average of F_1 plants with Ø4+5II				49.4
XT10 x Ert1	3	3	7II	61.4
XT10 x Ert14	3	3	7II	56.0
Ert1 x Ert14	2	4	7II	27.8
Ert1 x XT6	2	2	7II	65.0
Ert14 x XT6	3	3	7II	50.0
C1336 x XT4	1	3	7II	46.9
Ert47 x XT4	2	2	7II	62.7
Average of F_1 plants with 7II				52.8
Average				50.6

* Two of the diallel crosses were lost due to cutworm damage.

DISCUSSION AND CONCLUSION

The average per cent sterility at each of the interchange levels obtained in this study (Table 6) was higher than previous reports have indicated (Table 1). This may be due in part to the very small sized populations that most other workers studied, the particular interchanges involved, or environmental conditions at the time of flowering. Certainly in this study the per cent sterility varied a great deal from cross to cross within each interchange level. But crosses were grown at various times over a two year period, and even when they were planted at the same time, they did not flower at the same time. That barley fertility is extremely sensitive to environmental conditions was reported by Burnham and Hagberg (9). Therefore the effect of specific interchanges on sterility was confounded with environmental effects and further studies will have to be made to determine the importance of specific interchanges on sterility.

The application of the proposed "Oenothera" method to gamete selection in barley depends on a relatively high degree of fertility of interchange heterozygotes involving all chromosomes in interchanges. Nishimura et al. (34) and Nishimura and Kurakami (33) suggested the use of a 08+06 plant or 010+04 plant instead of a 014 plant. The fertility of the desired 08+06 plants was calculated to be 12.6 per cent, the product of the observed fertility of plants with 08 and that of plants with 06 (33). Two plants with 08+06 were

observed by Nishimura (32). One was fully sterile and the other had a fertility of 7.1 per cent. No conclusions regarding the fertility of heterozygotes of this type could be drawn from his results because of the small size of population that he studied. In the present study, the average sterility was 75.3 per cent for F_1 plants with 06, and 78.7 per cent for F_1 plants with 08. According to the method of calculation employed by Nishimura and Kurakami (33), the fertility of plants with 08+06 would be 0.25 x 0.21, or 5.3 per cent, which is only 42 per cent of that calculated by Nishimura and Kurakami (33). The sterility of plants with 06+204 configuration was even higher, having an average of 96.7 per cent. Nishimura (32) reported 73.0 to 92.4 per cent sterility of plants with 06+204. However, he studied only one spike from each of six plants. From the discussion above, it seems that the sterility of barley interchange heterozygotes involving all chromosomes in interchanges would be higher than 90 per cent, and very probably it may reach as high as 95 per cent. Such a high degree of sterility would necessitate a very large population in the application of "Oenothera" method and minimize the practical use of the method.

The position of the exchange in interchanged chromosomes can be determined by linkage studies. In plants where clear pachytene configurations can be successfully prepared, the breakage points can be determined cytologically to a

certain degree of accuracy. The first demonstration of this cytological technique was by McClintock (31) for a case of semisterility in maize. In barley, the pollen mother cells are smaller and the chromosomes are much thicker and longer at the pachytene and diakinesis stages than are those in maize, making it more difficult to analyze the configurations (9).

In the F_1 plants from a cross between interchange stocks involving the same two pairs of chromosomes, the manner of chromosome pairing at pachytene depends on the positions of breaks. This has been demonstrated by Turcotte (43) in maize. Although clear pachytene configurations were not obtained in the present study, the following discussion is important to understand the relative positions of exchange in different stocks involving interchange in the same chromosomes, and to explain the partial sterility obtained from their hybrids. Theoretically, if breakage points are identical in both stocks, the interchanged chromosomes would pair normally and there should be no adverse effect on fertility. If the breakage points are very closely located, normal pairing would be expected, but a minute deficiency would cause the abortion of some of the gametes. If breaks have occurred in the same arms but not closely located, T-shaped bivalents or bivalents with a loop would be seen. When one interchanged chromosome in both stocks has a breakage point in the same arm, and the other interchanged chromosome has the breakage

point in a different arm, a "T-shaped" or "looped bivalent" and an "H-shaped bivalent" would appear in the same cell. In the event that both interchanges occur in different arms of the same chromosomes in different stocks, two "H-shaped bivalents" would be seen if all the exchanged pieces are small; or, cross-shaped configurations would be formed if the exchanged segments are large. These cross-shaped configurations, although similar to those which form in the F_1 from the cross between interchange stocks and normals, would have intercalary loops or arms with open ends. At metaphase I the cross-shaped configurations will form a ring or chain of four chromosomes, whereas all the other types will be recognized as "bivalents". Hagberg (22) has demonstrated that seven "bivalents" were formed following the cross between barley interchange stocks involving the same two pairs of chromosomes. The same phenomena were observed by Turcotte (43) in maize. Therefore, if a ring of four is seen at metaphase in the F_1 from a cross between two different stocks involving the same two pairs of chromosomes in interchange, it is logical to assume that the positions of exchange in the two stocks are not located on the same arms of the interchanged chromosomes.

Based on this assumption and the observed metaphase configurations in the F_1 plants of diallel crosses, the (a-b) interchange stocks as well as the (c-f) interchange stocks can be divided into two groups. In the six (a-b) interchange stocks, all except XT12 belong to one group. In the (c-f)

interchange stocks, XT10, Ert1, Ert14, and XT6 fall in one group, and XT4, Ert47, and C1336 in the other. Tables 9 and 10 present the metaphase configurations of F_1 from all possible diallel crosses within both (a-b) and (c-f) interchange stocks. For those that have not been identified cytologically, the expected configurations, based on whether or not both parental stocks belong to the same group, are given in parentheses.

Unless the interchanged chromosomes which came from different (a-b) or (c-f) interchange stocks, and which appeared to pair normally at metaphase I, had identical breakage points, it would not be surprising to obtain a similar degree of sterility in crosses with and without ring formation. Some of the gametes which developed from pollen mother cells without ring formation were non-viable because of chromosomal deficiency-duplication. Assuming an independent separation of the chromosomes of the two seeming "bivalents" during anaphase I, half of the gametes would be non-viable and half viable, and a 50 per cent sterility is to be expected. The observed semi-sterility, which agrees with this assumption, leads to the conclusion that, except for C1384 and C1385, none of the breakage points in the different (a-b) or (c-f) interchange stocks are identical. The low sterility (12.2 per cent) in the F_1 of the cross C1384 x C1385 might suggest that the breakage points of "a" and "b" chromosomes in these stocks are identical. However, further evidence is necessary before a definite

TABLE 9. Observed and expected* metaphase configurations in the F_1's of (a-b) interchange stocks.

	XT12	Ert7	XT8	C1385	C1384
C1343	(04+5II)	7II	(7II)	7II	(7II)
C1384	04+5II	7II	7II	(7II)	
C1385	04+5II	7II	7II		
XT8	04+5II	7II			
Ert7	04+5II				

* The expected metaphase configurations are parenthesized.

TABLE 10. Observed and expected* metaphase configurations in the F_1's of (c-f) interchange stocks.

	XT4	Ert47	C1336	XT6	Ert14	Ert1
XT10	04+5II	04+5II	04+5II	(7II)	7II	7II
Ert1	04+5II	04+5II	04+5II	7II	7II	
Ert14	04+5II	04+5II	04+5II	7II		
XT6	04+5II	04+5II	04+5II			
C1336	7II	(7II)				
Ert47	7II					

* The expected metaphase configurations are parenthesized.

conclusion could be reached.

The phenomena discussed above should be taken into consideration in the future work of identifying new interchanges. If the unknown interchange is (c-f) and a stock with (c-f) interchange is used as a tester, either 04+5II and seven "bivalents" or only seven "bivalents" would appear in the F_1. If the worker is also interested in determining the relative positions of breaks in the unknown stock, it is advisable that the unknown be crossed with two (c-f) interchange stocks from different groups, for example, XT10 and XT6. If the F_1 of the unknown and either XT10 or XT6 is fully fertile, the breakage points would be identical in the unknown and the tester. If the semisterile F_1 of the unknown and XT10 gives rise to seven bivalents, and the F_1 of the unknown and XT6 shows ring formations at metaphase I, the breakage points in the unknown and XT10 are located on the same arms and that of the unknown and XT6 are therefore not located on the same arms of the same interchanged chromosomes. Situations may also arise where the F_1's from both testcrosses have no ring formations at metaphase I and are all semisterile. Then in the unknown the breakage point of one chromosome is located on the same arm as that of its homologue in XT10, and the breakage point of the other chromosome is located on the same arm as that of its homologue in XT6.

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APPENDIX. Designation, parental source and originating station of homozygous interchange stocks.

Stock designation	Chromosomes involved in interchange	Parental source	Originating station
C1343	a-b	Mars	University of Minnesota
C1384	"	"	"
C1385	"	"	"
XT8	"		Svalöf
XT12	"		"
Ert7	"	Gull	"
C1376#1	a-c	Mars	University of Minnesota
C1427	"	"	"
XT11	"		Svalöf
XT5	a-d		"
7031	"	Montcalm	University of Saskatchewan
C1456	a-e	Mars	University of Minnesota
XT16	"		Svalöf
XT18	a-f	Bonus	"
XT9	a-g		"
C1365	b-c	Mars	University of Minnesota
C1025	b-d	"	"
C1358	"	"	"
C1346	b-e	"	"
C1310	b-f	"	"
C1483	b-g	"	"
XT3	"		Svalöf
C1340	c-d	Mars	University of Minnesota
C1405	"	"	"
C1432	c-e	"	"
C1336	c-f	"	"
XT4	"		Svalöf
XT6	"		"
XT10	"		"
Ert1	"	Gull	"
Ert14	"	Maja	"
Ert47	"		"
XT1	c-g		"
XT13	"		"
XT15	d-f	Bonus	"
XT2	d-g	"	"
XT14	"		"

APPENDIX. (Continued)

Stock designation	Chromosomes involved in interchange	Parental source	Originating station
C1420	e-f	Mars	University of Minnesota
C1482	"	"	"
C1433	f-g	"	"
4256-1	a-c-d	"	"
II-4	(a-f)(b-g)	XT18 x C1483	University of Manitoba
III-15	(d-g)(c-e)	XT2 x C1432	"
III-22	"	"	"
VII-9	(a-f)(c-e)	XT18 x C1432	"
XVII-2	(a-b)(e-f)	Ert7 x C1420	"
XXXIX-14	(b-d)(c-f)	C1358 x Ert1	"